ECOLOGIE DES TRICOTS RAYES DE NOUVELLE-CALEDONIE

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Au delà d'un point critique dans un espace fini, la liberté décroît comme s'accroît le nombre. Cela est aussi vrai des humains dans l'espace fini d'un écosystème planétaire que des molécules d'un gaz dans un flacon scellé. La question qui se pose pour les humains n'est pas de savoir combien d'entre eux survivront dans le système mais quel sera le genre d'existence de ceux qui survivront.

Ce que ne comprend pas celui qui ignore tout de l'écologie, c'est qu'il s'agit d'un système. Un système ! Un système qui maintient une certaine stabilité qui peut être rompue par une seule erreur. Un système qui obéit à un ordre, à un processus d'écoulement d'un point à un autre. Si quelque chose vient à interrompre cet écoulement, l'ordre est rompu. Et celui qui ignore l'écologie peut ne pas intervenir avant qu'il ne soit trop tard. C'est pour cela que la plus haute fonction de l'écologie est la compréhension des conséquences.

Pardot Kynes
Premier écologiste d'Arrakis
Herbert (1970)

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INTRODUCTION

Les organismes vivants utilisent des ressources pour vivre, croître et se reproduire. Derrière ce lieu commun se cache une théorie importante en Ecologie : la théorie des Traits d'Histoire de Vie (voir Stearns 1992, par exemple). Selon cette théorie, les individus optimisent l'utilisation de ressources limitées (ressources alimentaires, habitat, mais aussi partenaire sexuel entre autres) afin de maximiser des traits tels que la croissance, la survie ou la reproduction. Dans le cadre de la théorie de la sélection naturelle, les individus favorisés sont ceux qui adoptent les stratégies d'acquisition des ressources les plus efficaces dans un environnement donné. Ce concept très simple est extrêmement puissant pour comprendre l'écologie et la variété des stratégies adoptées par les espèces, les populations ou les individus. Cette théorie est d'ailleurs centrale en Ecologie Evolutive (Stearns 1992).

Il existe néanmoins certaines complications, notamment, lorsqu'au moins deux espèces différentes utilisent les mêmes ressources dans un environnement donné. Comment des espèces concurrentes pour la ou les mêmes ressources peuvent optimiser l'utilisation de ces ressources et maximiser leurs traits d'histoire de vie respectifs ?

Cadre théorique initial

Les cas de coexistences d'espèces proches dépendantes des mêmes ressources sont nombreux et soulèvent des questions fondamentales. Par exemple, comment des espèces en compétition pour les mêmes ressources peuvent-elles coexister ? La théorie de la selection naturelle suggère que seule l'espèce la plus performante devrait résister aux processus de compétition. Confirmant cette notion, il existe des cas de ruptures de l'isolement géographique s'accompagnant de disparitions d'espèces par compétition (Jaeger 1970, Case 1991). Différents modèles théoriques fournissent des voies de recherche pour comprendre comment des espèces dépendantes des mêmes ressources coexistent malgré la promiscuité (Gotelli 1998). Toutefois, il existe peu d'études de terrain ayant permis de valider ou d'infirmer ces modèles (Schluter 1994, Grant 1999). La reconnaissance des mécanismes de

coexistence et leur compréhension restent souvent incomplètes du fait de lacunes taxonomiques et de la complexité extrême des interactions entre les différentes espèces et de nombreux facteurs environnementaux (Tokeshi 1999).

Malgré la complexité des relations mises en jeu, la coexistence implique très souvent des interactions fortes entre espèces, notamment des interactions compétitives pour lesquelles deux espèces (au moins) s'influencent négativement. Il existe trois conditions majeures pour reconnaître une situation de compétition (Tokeshi 1999) : différentes espèces partagent les mêmes ressources, les ressources partagées sont en quantités limitées, et les espèces impliquées sont affectées défavorablement par chacune des autres espèces au cours de l'acquisition des ressources. Les situations de compétition sont d'un grand intérêt en écologie car elles font partie des facteurs majeurs influençant la structure des communautés (Begon et al. 1986, Tokeshi 1999).

Le principe de l'exclusion compétitive stipule que "deux ou plusieurs espèces présentant des modes identiques d'utilisation des ressources ne peuvent continuer de coexister dans un environnement stable, la plus apte éliminant les autres" (Hardin 1960, Grover 1997). Lorsque deux espèces cohabitent, il doit donc exister quelques différences entre elles dans l'utilisation des ressources (May 1981). Le principe de l'exclusion compétitive fait appel à la notion de ressource limitante dont trois types principaux ont été évoqués (Schoener 1974) : l'espace (ou habitat) , les ressources trophiques (alimentaires) et le temps (les rythmes d'activité et d'utilisation de ces ressources). Plus les espèces sont similaires dans leur utilisation respective de ces ressources limitantes, plus leur coexistence est précaire (May 1981). Cependant, des réserves ont été émises par rapport au principe de l'exclusion compétitive. Putman & Wratten (1984) indiquent que ce principe ne serait théoriquement possible que si les espèces n'étaient pas souples face à la compétition. Ces auteurs soulignent que les espèces ont en fait des possibilités de réaction et peuvent s'adapter à la présence d'un compétiteur. Crawley (1986) suggère encore plus radicalement que le principe ne fonctionne pas : si son raisonnement est très

logique, les hypothèses qui l'accompagnent sont trop simplistes car l'environnement n'est uniforme ni dans l'espace, ni au cours du temps.

Par ailleurs, diverses études théoriques et de terrain suggèrent qu'il existe souvent des mécanismes de relâchement de la compétition en situation naturelle (Loreau & Ebenhoh 1994, Schluter 1994, Huisman & Weissing 1999). L'évitement, la réduction ou le relâchement de la compétition interspécifique peuvent ainsi permettre la coexistence entre espèces. Ces phénomènes de relâchement de compétition sont classiquement reliés au partage des ressources, où deux espèces occupant le même habitat et ayant des besoins similaires utilisent ces ressources de manière différente afin de diminuer la compétition directe (Schluter 1994, Grant 1999).

Malgré son caractère intuitif, la mise en évidence du partage des ressources comme base de la coexistence d'espèces est extrêmement difficile à démontrer. La séparation de niches s'accompagne d'adaptations différentielles entre les espèces, par exemple pour acquérir un type précis de nourriture (déplacement de caractères, Brown & Wilson 1956, Grant 1999). Comme dans la plupart des mécanismes se déroulant sur de grandes échelles de temps, il est souvent impossible de déterminer les causes et les conséquences. Des adaptations spécifiques sont-elles une conséquence, ou l'origine du partage des ressources ?
Plusieurs autres problèmes viennent compliquer la situation. Même en se focalisant sur les aspects trophiques, les interactions proies-prédateurs et les interactions inter- ou intra-spécifiques sont à l'origine de pressions de sélection synergiques ou antagonistes sur le développement de certains caractères trophiques dont il est très difficile de dégager l'effet propre. Les problèmes d'allométrie viennent encore compliquer la situation. Les gammes de variations d'un trait donné sont souvent assez limitées et les recouvrements entre les espèces très faibles voire inexistants, ce qui complique fortement les comparaisons inter-spécifiques. Par exemple, il existe de fortes différences de taille corporelle entre les différentes espèces d'ongulés herbivores qui coexistent dans les plaines de certains pays d'Afrique (Sinclair 2000).

Mais la taille corporelle influence la plupart des traits d'histoire de vie et est soumise à l'action de nombreuses pressions de sélection (Stearns 1992). Il est alors impossible de distinguer l'influence de la taille *per se* de celle de la réduction de la compétition et du partage des ressources.

Pour comprendre comment des espèces proches coexistent et identifier les mécanismes par lesquels ces espèces ont répondu aux pressions imposées par un potentiel compétiteur, les tricots rayés de Nouvelle-Calédonie présentaient, *a priori*, une conjoncture écologique avantageuse : il existe deux espèces taxonomiquement, morphologiquement et écologiquement très proches qui coexistent en Nouvelle-Calédonie. Leurs similitudes permettaient apparemment de s'émanciper de la plupart des problèmes auxquels les études de situation de coexistences ont été confrontées. Par exemple, les gammes de taille sont très étendues et se recouvrent largement entre les espèces. Le fait que des espèces soient morphologiquement très proches apporte un avantage majeur pour tester certaines prédictions (déplacement de caractères, par exemple). Dans le cas où les tailles sont très similaires, on peut s'attendre à ce que les possibles différences dans l'utilisation des ressources soient effectivement liées à des contraintes imposées par la coexistence et non à des différences allométriques importantes. En outre, ces reptiles se nourrissent de proies dont la taille limite leur capacité d'ingestion : les structures trophiques (longueur des mâchoires) déterminent la taille maximale des proies qu'ils peuvent consommer. Les serpents, à de rares exceptions, n'utilisent par leur bouche lors des combats intra-spécifiques ou lors des accouplements ; les caractéristiques des mâchoires sont bien limitées à leur rôle trophique. Ils avalent leurs proies en entier, celles-ci sont donc elles-mêmes mesurables après régurgitation forcée. L'étude de ces serpents présente d'autres avantages. Ce sont des "Central Place Foragers" : ils sont sédentaires et doivent retourner à terre entre leurs voyages alimentaires en mer, sur le même îlot, pour digérer, muer, se reproduire et se reposer (Shetty & Shine 2002a, b, c, d). La mise en évidence de situations d'allopatrie (absence d'une des deux espèces sur certains sites) offrait la possibilité d'étudier l'écologie de ces espèces lorsqu'elles sont

isolées de l'éventuel compétiteur, et donc d'appréhender les mécanismes à l'origine d'une telle situation de coexistence entre espèces proches.
L'émancipation des problèmes d'allométrie et la simplicité de la relation taille des proies/taille des mâchoires, indépendamment de différentes pressions de sélections (sexuelle, ou pour la fécondité, par exemple) offraient donc *a priori* un cadre simplifié, et donc privilégié, pour l'étude d'un cas d'espèces proches sympatriques.

Les tricots rayés de Nouvelle-Calédonie semblaient donc de très bons candidats pour comprendre non seulement comment ces espèces coexistent mais aussi quels sont les mécanismes à l'origine d'une telle situation de coexistence entre espèce proches.

Evolutions du sujet

Cependant, nous avons eu à faire à un rebondissement inattendu : l'examen minutieux de l'écologie des deux espèces sympatriques de tricots rayés de Nouvelle-Calédonie a très rapidement montré que, sous des apparences très semblables, ces animaux étaient en fait complètement différents. D'autre part, beaucoup d'informations manquantes (écologie et disponibilité de leurs proies par exemple) défavorisait les comparaisons de situations d'allopatrie et de sympatrie, alors que ce type de comparaison est fondamental pour comprendre les mécanismes sous-jacents à la coexistence. De plus une seule situation d'allopatrie apparente a été mise en évidence chez ces espèces. Dès lors, nous étions confrontés aux mêmes difficultés que dans la plupart des études sur la coexistence d'espèces proches. Dans la plupart des cas, il manque indéniablement un segment crucial du problème, qui empêche d'avoir accès aux relations de causalité (histoire phylogéographique, écologie ancestrale, existence de situations de sympatrie et d'allopatrie, Tokeshi 1999). Cette thématique unique nous est rapidement apparue fragile, alors que d'autres questions, multiples, émergeaient. Ces différentes questions nous ont permis de récolter des éléments de compréhension et nous avons suivi les nouvelles pistes d'exploration qui s'ouvraient.

Structure de la thèse

Quels que soit les rebondissements auxquels nous avons été confrontés, il était pertinent de conserver une approche comparative entre les deux espèces de tricots rayés sympatriques de Nouvelle-Calédonie. Même s'il manque certains segments qui auraient éventuellement permis de répondre à la question de départ (des différences entre ces espèces sont elles la cause ou la conséquence de leur coexistence ?), il est quand même possible d'identifier des éléments qui permettent de comprendre comment ces espèces coexistent. Examiner comment ces espèces proches utilisent leurs ressources reste une voie d'investigation prioritaire en écologie ; et c'est donc sous cette approche comparative que se sont placés la plupart des travaux de cette thèse. Néanmoins, quelques résultats imprévus au départ sont venus compléter chacun des volets examinés. Globalement, outre cette introduction, la thèse est composée de cinq grandes parties (II-Matériels et méthodes d'études, III-Description des tricots rayés, IV-Ecologie marine, V-Ecologie terrestre et VI-Synthèse et perspectives).

La première étape indispensable concerne la description de ces animaux. En effet, le couple d'espèces sympatriques étudié au cours de cette thèse (les tricots rayés de Nouvelle-Calédonie) était extrêmement peu décrit, raison pour laquelle il était admis que ces deux espèces avaient des écologies très similaires. Une première brève étude avait eu lieu sur les tricots rayés de Nouvelle-Calédonie, il y a une quarantaine d'années (Saint Girons 1964). Un livre résumait l'état des connaissances glanées principalement au cours de plongées (Ineich & Laboute 2002) et quelques études avaient été publiées sur des espèces différentes et dans d'autres localités (Pernetta 1977, Glodek & Voris 1982, Voris & Voris 1983, Stuebing & Voris 1990, Guinea 1986, 1991, Lading et al. 1991, Voris & Voris 1995, Heatwole 1999, Shine & Shetty 2001a,b, Reed et al. 2002, Shetty & Shine 2002a,b,c,d, Shine et al. 2002a,b, Heatwole et al. 2005, Cogger & Heatwole 2006). Le projet d'étude des tricots rayés de Nouvelle-Calédonie, sur lequel s'appuie cette thèse, débuté en 2002, a donné lieu à quelques publications (Shine et al. 2003a,b, Bonnet et al. 2005).

Un pré-requis avant de pouvoir comparer des espèces est de connaître leur écologie. Les tricots rayés sont amphibies et utilisent le milieu marin et le milieu terrestre pour des activités bien différentes. Le milieu marin est dédié à la recherche de nourriture, alors qu'à terre s'effectuent toutes les autres activités de la vie de ces animaux. Une fois la première étape de description générale de ces animaux accomplie, il est plus aisé d'examiner les tricots rayés plus en détails, en scindant leur écologie en fonction de leurs milieux de vie respectifs.

Le deuxième chapitre concerne l'écologie marine de ces animaux. Ce volet est crucial car c'est dans ce milieu que les tricots rayés acquièrent leur nourriture en plongeant pour capturer des proies benthiques. Les ressources alimentaires sont prépondérantes dans les situations de coexistence (Tokeshi 1999) et les espèces sympatriques présentent généralement des différences dans l'utilisation des ressources alimentaires (Schluter 1994, Grant 1999). Dans notre cas, on s'attend à ce que les deux espèces de tricots rayés divergent dans les milieux de chasse prospectés et/ou les proies consommées, et c'est donc ces paramètres que nous avons examinés dans ce chapitre.
En outre, les données récoltées nous ont rapidement poussés à aborder le problème sous un angle qui n'était pas évident au départ : le rôle des tricots rayés dans l'écosystème lagonnaire. Ce rôle, central, mène assez naturellement à des questionnements en terme de conservation. Les tricots rayés apparaissent comme de bons bio-indicateurs de biodiversité et cette partie occupe une place non négligeable au sein du deuxième chapitre.

Le troisième chapitre concerne l'écologie terrestre des tricots rayés. La vie à terre de ces animaux est principalement dédiée à la digestion des proies capturées en mer, à la mue et à la reproduction (accouplement et ponte). Toutes ces activités nécessitent des conditions particulières. Les tricots rayés comme tous les serpents ont besoin de thermoréguler en fonction des températures disponibles dans l'environnement et de leurs besoins métaboliques. Les tricots rayés doivent donc sélectionner précisément l'habitat terrestre qui présente des gammes de température

adéquates pour accomplir des activités particulières. Si les deux espèces ne présentent pas les mêmes affinités thermiques, on peut s'attendre à ce que chaque espèce sélectionne des habitats terrestres différents. Alternativement, si les deux espèces présentent les mêmes affinités thermiques, on s'attend alors à ce qu'elles partagent le même habitat. Enfin, des différences dans leurs capacités locomotrices (reptation, escalade, Bonnet et al. 2005) vont vraisemblablement se traduire par des différences dans l'utilisation de l'habitat terrestre.

Par ailleurs, nous avons également examiné une contrainte majeure associée à la vie insulaire de ces animaux en Nouvelle-Calédonie : l'absence d'eau douce et les stratégies développées par ces deux espèces pour en acquérir.

Enfin, une synthèse des principaux résultats et des perspectives permettront d'ouvrir ce travail vers d'autres voies d'exploration.

NOTE

La structure sur articles, pour laquelle j'ai opté dans ce manuscrit, impose malheureusement quelques lourdeurs qui lui confèrent un aspect un peu dégingandé. D'abord, le lecteur devra assez régulièrement passer de parties rédigées en Français (l'Introduction par exemple) à des parties rédigées en Anglais (les articles). De la même manière, le style de rédaction est forcément bien différent entre ces éléments. Toutefois, cette lourdeur pour des lecteurs francophones devient très avantageuse pour des lecteurs étrangers (présents dans le jury par exemple). Les informations principales qui doivent être tirées de ce manuscrit se trouvent dans les articles, facilement accessibles pour des lecteurs étrangers.

Par ailleurs, l'ordre dans lequel j'ai décidé d'agencer les différents articles ne correspond absolument pas à l'ordre de publication original. Le succès de publication est assez aléatoire et met en jeu à la fois des aspects liés à la qualité du travail soumis (manque d'approfondissement ou de recul, précipitation lors de la rédaction et de la soumission,…) mais aussi des problèmes liés au système de publication (lenteur du processus, chance et quelquefois une certaine subjectivité du jugement des arbitres ou des éditeurs…). Il en résulte parfois des situations incongrues. Par exemple, lorsqu'un article fait référence à un travail publié précédemment mais placé ultérieurement dans le manuscrit.
En outre, certains travaux, en cours de rédaction, auront forcément un caractère inachevé.

Enfin, la partie "Matériels et Méthodes" de cette thèse sera assez succincte. En effet, les modèles d'étude sont présentés en détails dans un article dédié à la description de la morphologie et des principaux traits d'histoire de vie des tricots rayés de Nouvelle-Calédonie (Article 1, Chapitre I). Les sites d'études et méthodes sont, quant à eux, décrits en détails dans la section "Matériels et Méthodes" de

chaque article. Ainsi, cette partie me permet surtout de donner au lecteur les informations qui ne sont pas détaillées dans les articles.

Je suis bien conscient que ces acrobaties seront parfois lourdes pour le lecteur mais je crois que c'est malheureusement un des impondérables de la rédaction d'une thèse sur articles.

MATERIELS ET MÉTHODES D'ÉTUDE

Modèles d'étude

Position taxonomique

La position des serpents marins reste encore assez floue et est ardemment discutée par les spécialistes. Afin d'éviter de lister toutes les possibilités et garder cette partie relativement courte, j'ai décidé d'aborder brièvement cet aspect d'après le travail de J.S. Keogh (1998, Fig 1).

Bien qu'il existe quelques formes marines appartenant aux familles Acrochordidae et Colubridae, les serpents marins les "plus marins" appartiennent tous à la sous-famille des Hydrophiinae, au sein de la famille des Elapidae (Fig 1).

Cet ensemble de serpents marins est composé de deux sous-groupes facilement distinguables : (i) les Hydrophiinae, qui sont strictement inféodés au milieu marin et (ii) les serpents du genre Laticauda, qui sont amphibies.

Laticauda : les serpents marins amphibies

Ce type de serpents marins est particulier par son mode de vie amphibie. Les Laticauda restent liés au milieu terrestre. Ils vont se nourrir en mer mais reviennent à terre pour toutes les autres activités (accouplement, ponte, mue, digestion, repos…, Heatwole 1999). Comme tous les serpents marins (et la plupart des reptiles marins), ces animaux sont inféodés à la ceinture tropicale, probablement pour des raisons thermiques. Les Laticauda sont présents sur la plupart des milieux récifaux des Océans Indien et Pacifique Ouest (Heatwole 1999, Ineich & Laboute 2002).

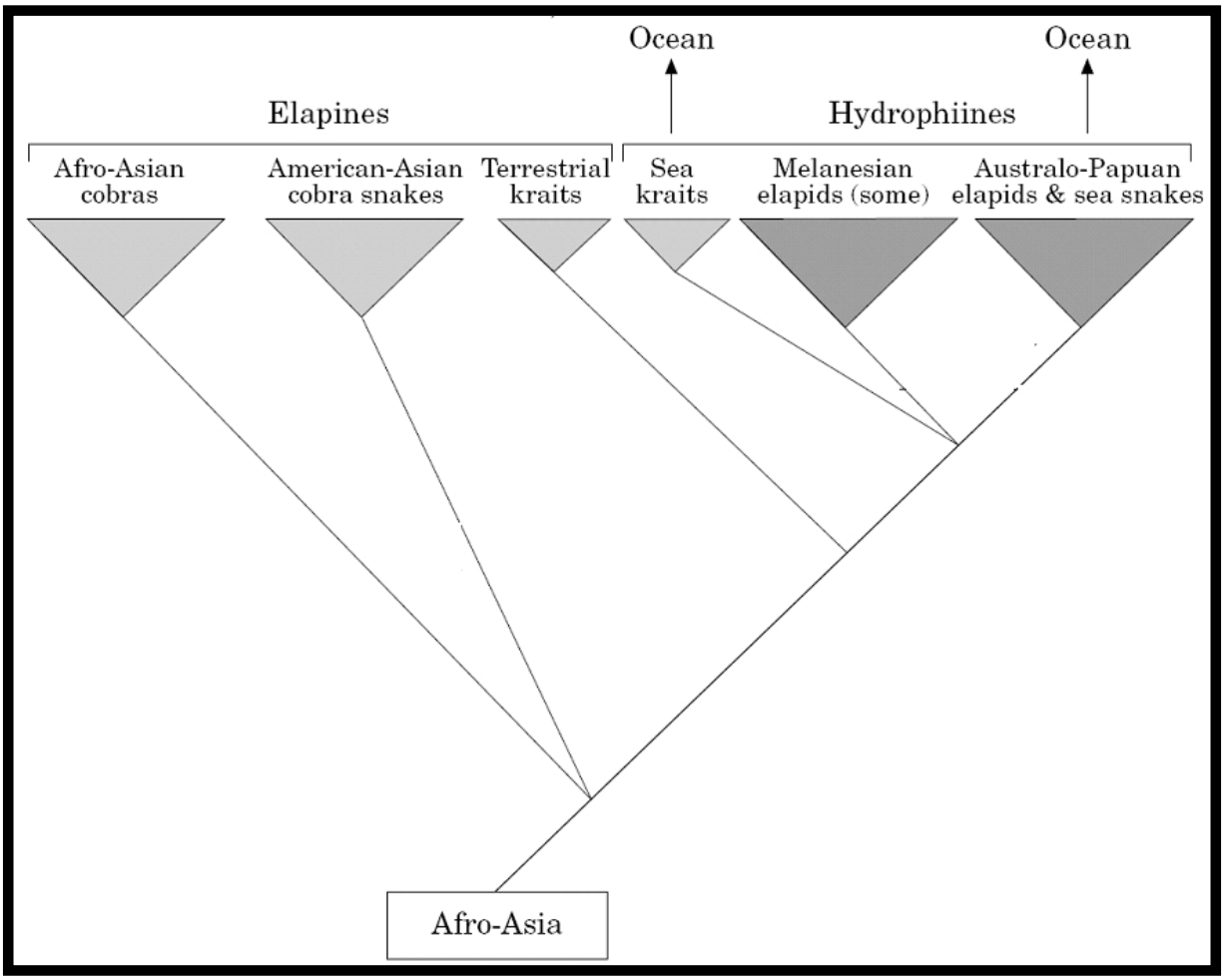

FIG. 1 – Biogeographic relationships of the major elapid clades. This representation supports two independant origins of invasion of the aquatic environment, one in the partially aquatic sea kraits, another in the diverse radiation of the fully aquatic true sea snakes. Reproduced from Keogh (1998).

J'ai listé dans cette sous-partie toutes les espèces (8) actuellement reconnues de Laticauda, associées à leurs répartitions géographiques respectives (Heatwole et al. 2005, Cogger & Heatwole 2006). Les vastes répartitions géographiques de *Laticauda colubrina* et *L. laticaudata* ainsi, qu'a plus faible échelle celle de *L. semifasciata*, laissent peu de doutes sur le fait que de multiples espèces sont réunies sous ces dénominations.

Les études récentes soulignent trois complexes majeures (Heatwole et al. 2005, Cogger & Heatwole 2006).

Le complexe *L. colubrina*

Laticauda colubrina, dont l'aire de répartition est extrêmement large, du Golfe du Bengale, à travers l'archipel Est-Indien et la Nouvelle-Guinée, vers l'Est jusqu'aux îles du Pacifique Sud-Ouest, vers le Nord à travers les Philippines, Palau et Taïwan jusqu'à l'archipel des Ryukyu au sud du Japon (Est-Ouest 11 000 Km ; Nord-Sud 7 000 Km !).
Laticauda frontalis, endémique du Vanuatu et des Iles Loyauté.
Laticauda guineai, récemment décrit, endémique de Nouvelle-Guinée.
Laticauda saintgironsi (Fig 2), récemment décrit, endémique de Nouvelle-Calédonie.

Le complexe *L. laticaudata*

Laticauda laticaudata (Fig 2), dont l'aire de répartition est extrêmement large, du golfe du Bengale, à travers l'archipel Est-Indien et la côte asiatique Sud-Est, au Nord à travers les Philippines et Taïwan jusqu'au Sud du Japon, et vers l'Est à travers La Nouvelle-Guinée et les îles Salomon jusqu'aux îles du Pacifique Sud-Ouest (Est-Ouest 10 500 Km ; Nord-Sud 7 000 Km !).
Laticauda crockeri, endémique au lac Te-nggano (saumâtre) sur l'île Rennell dans les Salomon.

Le complexe *L. semifasciata*

Laticauda semifasciata, du Sud du Japon, à travers Taïwan et les Philippines jusqu'à quelques îles à l'Est de l'Indonésie.
Laticauda schistorhyncha, endémique à l'île Niue.

Les Laticauda de Nouvelle-Calédonie : Les tricots rayés

En Nouvelle-Calédonie, sont présentes deux espèces de *Laticauda*, appelées localement tricots-rayés. Il s'agit de *L. saintgironsi* (le tricot-rayé jaune, endémique, Cogger & Heatwole 2006 ; Fig 2) et de *L. laticaudata* (le tricot-rayé bleu ; Fig 2). Ces animaux sont les plus austraux de tous les Laticauda, la Nouvelle-Calédonie étant la limite Sud de répartition de ce groupe.

FIG. 2 – The two sea krait species from New-Caledonia: the tricots rayés. Upper pictures *L. saintgironsi*, yellow sea krait; lower pictures *L. laticaudata*, blue sea krait (© XB, FB).

Sites d'étude

La Nouvelle-Calédonie

La Nouvelle-Calédonie est un ensemble d'îles et d'archipels mélanésiens de l'Océan Pacifique sud, situé autour des coordonnées 21°30'S 165°30'E, à environ 1 200 Km à l'est de l'Australie et 1 500 Km au nord-est de la Nouvelle-Zélande (Fig 3).

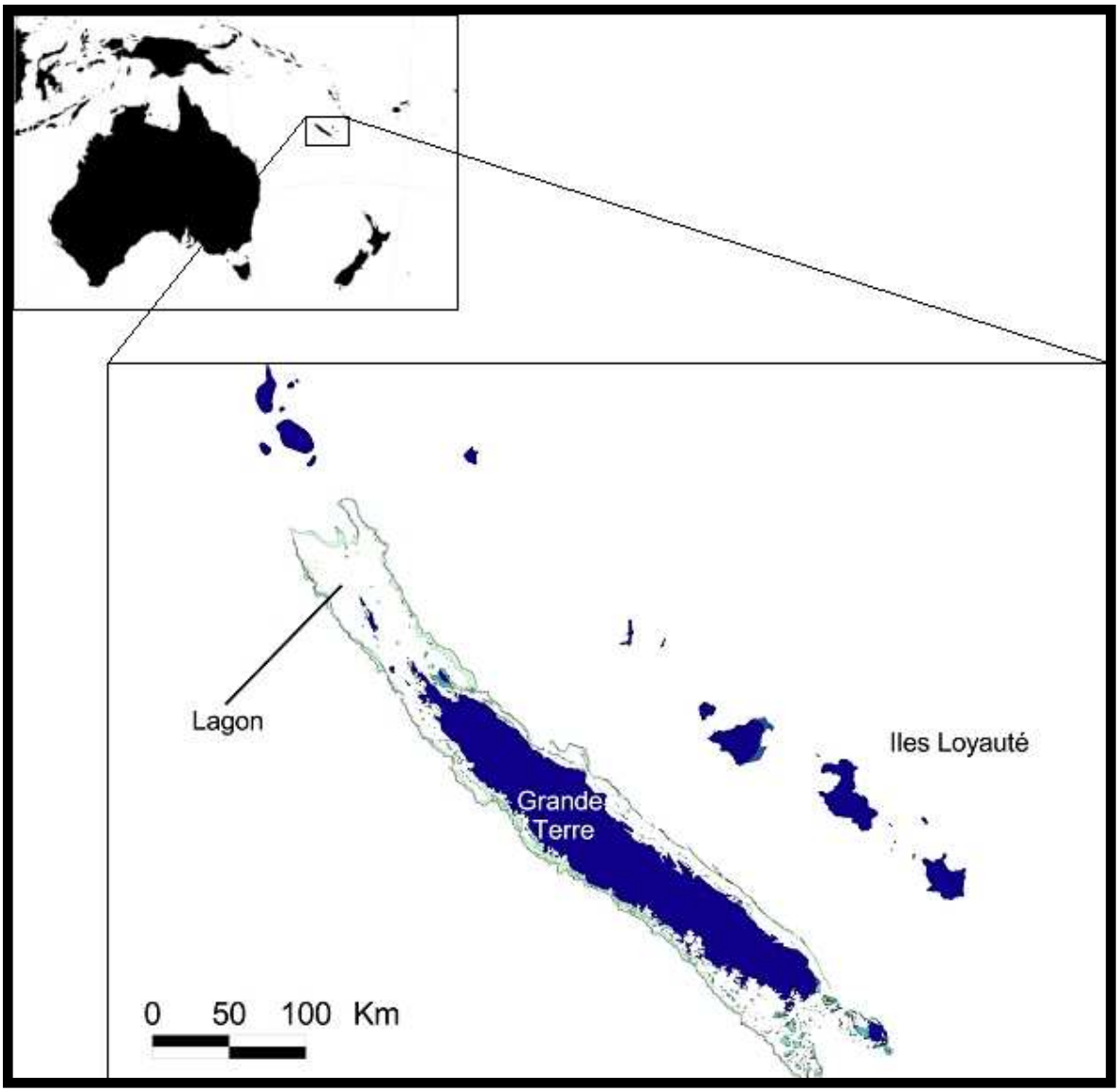

FIG. 3 – Global map of New-Caledonia. Dark-blue areas represent the emerged land (Main land and islets) ; light-blue areas, the reef flats and light-green areas the barrier-reef and the fringing reefs.

La Nouvelle-Calédonie est constituée d'une île principale (Grande Terre) et de plusieurs ensembles d'îles plus petites, les îles Belep au Nord de la Grande Terre, l'île des Pins au Sud, les îles Loyauté à l'Est (Ouvéa, Lifou, Tiga et Maré), ainsi que d'un grand nombre d'îlots situés entre la Grande Terre et le récif-barrière. Sur une superficie de 16 372 Km², la Grande Terre s'étire du Nord-Ouest au Sud-Est sur près de 400 Km en longueur et 50 à 70 Km en largeur.

Le lagon calédonien a une surface totale de 24 000 Km², ce qui en fait l'un des plus grands lagons du monde. Il est ceinturé par une barrière de corail (récif-barrière) d'une longueur de 1 600 Km, située entre 10 et 50 Km des terres.

Le lagon Sud-Ouest et les sites d'études

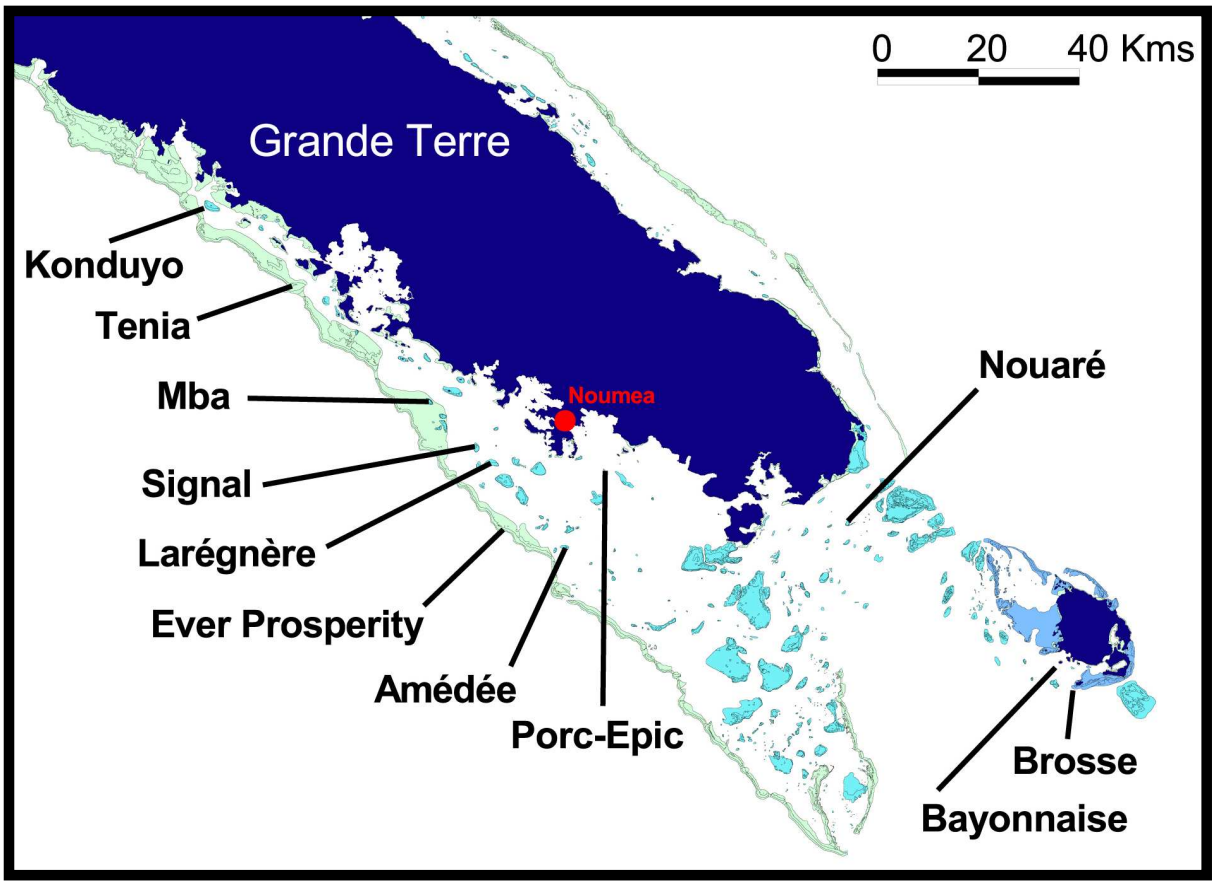

FIG. 4 – The South-West Lagoon of New-Caledonia. Dark-blue areas represent the emerged land (Main land and islets) ; light-blue areas, the reef flats and light-green aresa the barrier-reef and the fringing reefs.

FIG. 5 – Pictures of some of the study sites. From top to bottom and from left to right: Signal, Larégnère, the Ever-Prosperity (on the barrier-reef), Amédée (the barrier-reef is visible on the upper part of the picture), Porc-Epic (rocky and steep) and Nouaré (© Isabelle Joly).

Pour des raisons essentiellement logistiques (présence de réserves, proximité de Nouméa, facilité des trajets en bateaux…), nos sites d'étude se trouvent principalement dans le Lagon Sud-Ouest (Fig 4). Il s'agit de la zone la plus large du lagon de Nouvelle-Calédonie, la distance entre la côte de la Grande Terre et le récif-barrière dépassant 30 Km au Sud de Nouméa.

Les îlots d'études sont parsemés entre le récif-barrière et la Grande Terre sur une distance d'environ 200 Km du Nord au Sud (Fig 4). Les sites d'étude sont constitués de 9 îlots naturels (du Nord au Sud, Konduyo, Ténia, Mba, Signal, Larégnère, Porc-Epic, Amédée, Nouaré, Bayonnaise et Brosse, Fig 4, 5, Table 1). Nous avons aussi visité un site très particulier : l'Ever-Prosperity, épave d'un bateau échoué sur la barrière.

Tous ces sites présentent une morphologie particulière (superficie, type de substrat, végétation, altitude, Fig 5) et un environnement différent (superficie et profondeur du platier corallien, distance à la Grande Terre ou au récif-barrière, Fig 4, 5).

Au final, ces sites ont été visités entre 1 et 14 fois par 1 à 5 personnes au cours des 4 années d'étude (Table 1).

Méthodes générales

Captures

Les tricots rayés sont le plus souvent visibles quand ils traversent la plage, en déplacement entre le lagon et la terre. Le périmètre de chaque îlot a été parcouru de jour et de nuit. L'intérieur de chaque site a également été régulièrement examiné. La plupart des serpents ont été capturés à la main, maintenus en sac de coton jusqu'aux mesures et relâchés de 1h à 24h après capture (Fig 6).

Les détails concernant les captures sur chacun des sites d'étude sont présentés dans le Tableau 1.

TABLEAU 1 – Details of the different field trips. The study sites, sampling periods, the number of captured snakes and the field workers are given for each field trips. LL : *L. laticaudata*, LS : *L. saintgironsi*; number of captured snakes.

Site	Period	# days	LL	LS	Team[1]
Amédée	Dec 2002	1	4	25	II, RS, XB
	Feb 2005	3	89	86	AL, FB, OH, XB
	Apr 2005	7	83	102	FB
	May 2005	5	63	79	FB
	Nov 2005	7	172	181	FB, MDC
	Feb 2006	5	80	99	DP, FB, MDC, SL
	Nov 2006	5	125	183	AR, FB, MS, XB
Total		**33**	**616**	**755**	
Bayonnaise	Dec 2003	5	59	70	FDR, II, JH, XB
Brosse	Nov 2003	4	8	120	FDR, II, JH, XB
Ever-Prosperity	Feb 2005	0.25	1	43	AL, EP, FB, OH, XB
Konduyo	May 2005	4	0	0	FB
Larégnère	Feb 2005	5	19	113	AL, FB, OH, XB
	Apr 2005	5	4	71	FB
Total		**10**	**23**	**184**	
Mba	Mar 2005	7	66	61	FB
Nouaré	Dec 2002	3	0	50	II, JH, XB
Porc-Epic	Jan 2002	1	6	8	HC, II, RS, XB
	Dec 2002	3	52	31	II, JH, XB
	Nov 2005	5	70	108	FB, FB-2, MDC
	Dec 2006	4	99	65	FB, MG
Total		**13**	**227**	**212**	
Signal	Jan 2002	1	22	21	HC, II, RS, XB
	Nov 2002	4	129	78	II, JH, XB
	Dec 2002	1	52	30	II, JH, XB
	Dec 2002	1	48	33	II, JH, XB
	Nov 2003	9	165	143	FDR, II, JH, XB
	Feb 2004	7	79	47	FB
	Mar 2004	21	400	160	FB
	Jan 2005	14	617	173	AL, FB, OH, OL, XB
	Mar 2005	6	56	60	FB
	Jun 2005	5	35	92	FB
	Dec 2005	45	1 898	771	FB, MDC, SL, TB
	Feb 2006	13	505	178	FB, MDC, SL
	Nov 2006	15	215	195	FB, XB
	Dec 2006	6	184	207	FB
Total		**148**	**4 405**	**2 188**	
Ténia	Feb 2005	5	26	62	AL, FB
Total		**233**	**5 431**	**3 745**	

1, AL : Amanda Lane, AR : Amélie Ramirez, DP : David Pearson, EP : Eric Potut, FB-2 : Franck Boulleret, FDR : François De Riberolles, HC : Al Cogger, II : Ivan Ineich, JH : Julie Halatas, MDC : Margot De Crignis, MG : Michael Guillon, MS : Marina Shépaçonhom, OH : Mayol, OL : Olivier Lourdais, RS : Rick Shine, SL : Sophie Lorioux, TB : Thomas Barreau, XB : Xavier Bonnet

Mesures diverses

Mesures biométriques et description

Pour chaque serpent, l'espèce, le sexe et la classe d'âge ont été déterminés. Chaque serpent a été mesuré en longueur avec un mètre à ruban (longueur museau-cloaque [snout-vent length, SVL], longueur de la queue, ±1cm ; Fig 6) et pesé avec une balance électronique (±1g).

Un certain nombre d'autres mesures a été effectué au niveau de la tête (longueur du crâne, largeur de la tête, diamètre des yeux et longueur de la mâchoire, ±0.01mm) ou de la queue (largeur et hauteur, ±0.01mm).

Les animaux ont été minutieusement examinés, nous avons notamment compté le nombre d'anneaux noirs (corps et queue) et relevé la présence d'anomalies de coloration. Les cicatrices, parfois nombreuses, ont été décrites (forme et taille). La présence de tiques (*Amblyomma laticaudae*, spécialisées sur les tricots rayés, Fig 6) a été notée ainsi que le stade de développement (larve, nymphe, adulte) ou le sexe (uniquement pour les adultes).

Palpation, alimentation et reproduction

L'abdomen de chaque individu a été minutieusement palpé afin de déterminer la présence de proie ou le statut reproducteur (pour les femelles).

Lors de la détection d'une proie, comme les tricots rayés se nourrissent essentiellement de poissons sans nageoire rigide, il a été facile de faire régurgiter les animaux doucement sans risque de blessure (Fig 6). Dans quelques occasions, des poissons-chats (*Plotosus lineatus*) ont posé quelques difficultés mais la régurgitation a été possible avec beaucoup de soin et de patience.

En une seule occasion, la régurgitation forcée a provoqué la mort de l'animal : une dent du crâne digéré d'une murène a apparemment coupé un vaisseau sanguin,

entraînant une hémorragie fatale. Si ce n'est ce cas, nous n'avons jamais observé de troubles liés à la régurgitation forcée. Comme la perte d'un bol alimentaire n'est jamais anodine, nous avons pris soin de ne faire régurgiter les individus qu'une seule fois au cours de leur histoire de captures.

Les proies ont été mesurées (longueur du corps, de la queue, ±0.5cm ; diamètre au niveau de la tête, du milieu du corps et du cloaque, ±0.01mm) et conservées dans l'alcool afin d'être identifiées au laboratoire.

Dans la plupart des cas, si la proie n'était pas régurgitée, ses mensurations à l'intérieur du serpent ont été mesurées (longueur ±1cm, diamètre ±0.01mm), les couches tissulaires (estomac, côtes) distendues rendant les mesures suffisamment précises.

En ce qui concerne la reproduction, l'abdomen des femelles adultes a été palpé pour détecter d'éventuels follicules en développement ou œufs ovulés, ces deux stades étant facilement reconnaissables à la palpation. Nous avons aussi observé un certain nombre de comportements de reproduction et accouplements pour les deux espèces (Fig 6). Les périodes de reproduction ont été inférées de ces données.

Marquage

La plupart des individus ont été individuellement marqués de manière permanente par coupure et brûlure superficielle d'écailles ventrales, le tatouage à chaud induisant un changement de couleur des écailles visées (Fig 6).

FIG. 6 – Some illustrations of the field work. From top to bottom and from left to right. Snakes in transit on the shore (ready to be captured!), SVL measurements, copulating *L. laticaudata*, infestation by ticks *A. laticaudae* (5 adult females and 1 reddish male), forced regurgitation of *Gymnothorax fimbriatus* by *L. saintgironsi*, iron branding and marks after healing (black marks in the blue bands). (© XB, FB, Stéphane Bignon).

Récapitulatif

Nous avons observé 9 176 serpents (animaux non-marqués, captures et recaptures). Le nombre total de serpents marqués est de 4 714 (2 161 *L. laticaudata* et 2 553 *L. saintgironsi*) avec 4 333 recaptures (3 163 *L. laticaudata* et 1 170 *L. saintgironsi*, entre 1 et 23 recaptures par individus).
Nous avons obtenu 1 077 proies régurgitées dont la liste est donnée dans les articles 1 (Chapitre I), 3, 4, 6 et 7 (Chapitre II).

Au total, nous avons mesuré 6,5 kilomètres et pesé 1,4 tonnes de serpents (et compté 256 000 anneaux noirs) et mesuré 180 mètres et pesé 22 kilogrammes de murènes…

Chapitre I

DESCRIPTION DES TRICOTS RAYÉS DE NOUVELLE-CALÉDONIE

Life history of sea kraits in New Caledonia

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Abstract. Two species of sea kraits (Laticaudidae) occur in New Caledonia. The yellow sea krait *Laticauda saintgironsi*, closely related to *L. colubrina* and *L. frontalis*, is endemic to the area. The blue sea krait (*L. laticaudata*) is widespread over the west Pacific, however an absence of careful taxonomic studies impedes to determine to what extent it might be also an endemic species. Paradoxically, despite their abundance, there is very little scientific information on the neo-caledonian sea kraits. Since 2002 we set up a mark recapture study on 10 islets. We gathered the most comprehensive data set on the morphology and ecology of these two species of snake. We captured and individually marked more than 4,000 snakes, and gathered more than 3,000 recaptures. We provide the mean values for the body size, body mass, number of rings of the two species. We also present the first information about the reproduction phenology. Despite superficial similarities, we detected significant difference between the two species for all the characteristics we investigated.

1 INTRODUCTION

Sea kraits (Hydrophinae, Laticaudidae) are among the most widespread sea-snakes. Large numbers occur over a geographic area broadly limited by India, Tongan archipelago, Japan and New Caledonia (Greer 1997; Heatwole 1999). Such a wide distribution range offers ample opportunities to examine variations between contrasted environmental conditions within a narrow taxonomic range. In addition, sea kraits are characterised by an amphibious life style. They forage at sea, court, mate, lay their eggs, digest, rest, slough their skin on land (Greer 1997; Heatwole 1999). The respective constraints of these two contrasted environments generate conflicting selective forces, notably to optimise locomotor performances at sea versus on land (Shine & Shetty 2001b; Shine et al. 2003b). Sea kraits are docile animals, easy to catch and to handle. Overall, sea kraits are interesting biological models to address several major evolutionary questions. Despite such combination of logistical and scientific advantages to set up studies on these species (high population densities, easiness of capture and for handling, paradisiacal study sites…), relatively little information is available on the ecology of the sea-kraits. Recently, two species (*L. colubrina* and *L. frontal*is) have been examined in detail in two localities, Vanuatu and Fidji (Shine & Shetty 2001a, b, Shetty & Shine 2002a, b, c, d, Reed et al. 2002, Shine et al. 2002a, b, Shine et al. 2003a,b). These studies confirmed that the peculiarities of the ecology of the sea kraits constitute an excellent substrate to explore important issues such as speciation, trade-offs between marine and terrestrial locomotor performances, diet, activity pattern on land, or sexual dimorphism for instance (Shine & Shetty 2001a, b, Shetty & Shine 2002a, b, c, d, Reed et al. 2002, Shine et al. 2002a, b, Shine et al. 2003a,b). However, many other major characteristics such as population dynamics, foraging ecology, growth rates, phenology of reproduction, annual variations for all life history traits for example, remain virtually not documented. Given the limited number of field studies there

are very poor possibilities for comparisons between species and geographic areas over the distribution range of the sea kraits.

In New Caledonia, situated at the extreme south of the distribution range, two species of sea-kraits coexist: *Laticauda saintgironsi* (yellow sea krait, tricot rayé jaune) and *L. laticaudata* (blue sea krait, tricot rayé bleu). A single short term study provided preliminary data on the ecology of these two snake species (Saint Girons 1964). A book (Ineich & Laboute 2002) reviewed all the information available on the sea-snakes of New Caledonia, and in fact revealed a total cessation of investigation since the pioneer work of Saint Girons. Based on precise morphological criteria, Cogger and Heatwole (2006) shown that *L. saintgironsi*, formerly regarded as part of the wide-ranging *L. colubrina*, was an endemic species to New Caledonia. The blue sea-krait, *L. laticaudata*, is also a widespread species (occurring on many islands of the indo-pacific). This snake exhibit marked variations across its distribution range. It should be noted that owing to a lack of careful morphological, ecological and genetic study, the taxonomic status of this species remains unclear.

Since 2002, in collaboration with the University of Sydney (Australia) and the Muséum National d'Histoire Naturelle (Paris, France), we (CNRS, France) initiated a long term mark-recapture study on both species and we collected the most comprehensive data set available for this geographic area. In this paper, we present basic ecological data that aim to serve as a basis for future studies. Nonetheless, the large sample sizes on which we based the current analyses enabled to present new findings, to update previous data, and also to correct numerous errors that are still widespread in the scientific literature.

2 MATERIAL AND METHODS

2.1 Study site

All the study sites are situated in the south west lagoon. We surveyed 10 natural islets and an artificial one (a wreck lying on the barrier reef). The following sites, presented from the north to the south, have been visited on one to seven occasions (Figure 1): Konduyo, Tenia, Mba, Signal, Larégnère, Amédée, Porc-Epic, Nouaré, Bayonnaise and Brosse. We also visited on two occasions the wreck of the Ever Prosperity which stands on the barrier reef near Amédée islet (Figure 1). Across the different sites, marked variations occur in terms of geomorphology, proportions of sandy beaches *versus* coral cliffs, vegetation, surface area, location between the main island and the barrier reef or human frequentation. Such diversity enables to better appreciate local variations and hence to obtain a general picture of the species under focus. The study sites were regularly surveyed in 2002, 2003, 2004, 2005 and 2006 by one to four peoples. We spent a total number of 199 days of surveys. In November 2002 a capture-mark-recapture program was set up with several hundreds of snakes individually and permanently marked (by XB from the CNRS, and Ivan Ineich from the MNHN) essentially on Signal island, but also to a lesser extent on Porc-Epic, and Amédée islets. The CMR program was intensified and extended the following year to Nouaré, Bayonnaise and Brosse (XB, II), and then to Konduyo, Tenia, Mba, and Larégnère in 2004, 2005 and 2006 (FB, XB).

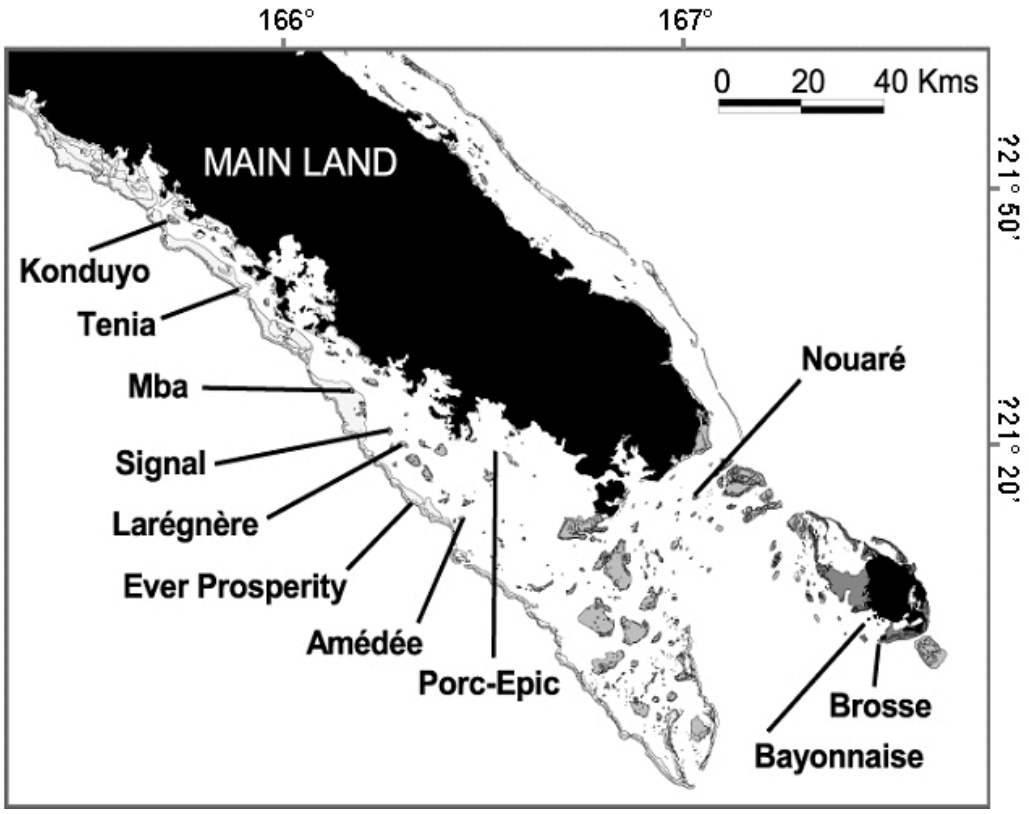

FIG. 1 - *Study area: the South-West lagoon of New Caledonia. Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by the light grey areas.*

2.2 Captures and measurements

As the snakes are mostly visible when they cross the shore, moving between the sea and the land, the whole perimeter of each islet was surveyed, both during the day and at night. The inland was also regularly surveyed. Most of the snakes were captured by hand and kept in cotton bags until processed. They were released after completion of the measurements 1h to 24h after capture. For each individual, the species, the sex, and the age class were recorded. We measured the size, snout vent length (SVL, ±1cm) by gently stretching the snake over a flexible ruler; the body

mass (±1g) was gathered with a portable electronic scale. We carefully examined each animal, notably to count the number of black rings, the occurrence of abnormalities of the colouration, the number, the size and the shape of scares, we also counted the visible external parasites (ticks) and recorded a number of morphological details (see results and discussion). Most of the snakes were individually and permanently marked by scale clipping coupled with iron branding that often provokes a change in the colouration of the scales targeted. We noted an interesting divergence between the two species: iron branding entailed a colour change from black to white and from blue to black in the blue sea krait; but a change from yellow to dark orange and no change for the black scales in the yellow sea krait. A small proportion of the snakes were only observed by sight, notably during behavioural investigations, both on land or under water. The total number of snakes observed, pooling captures + recaptures, over the study period was 7,917 (4,823 *L. laticaudata* and 3,094 *L. colubrina*). The total number of individually marked snakes was 4,114 (1,913 *L. laticaudata* and 2,201 *L. colubrina*) with 3,598 recaptures (2,827 *L. laticaudata* and 771 *L. colubrina*). These values are among the highest for snake ecology, and given the fact that we set up the program in 2002, they show that the sea kraits of New Caledonia represent one of the best systems as stated in the introduction.

2.3 Feeding habits

The abdomen of each snake captured was carefully palpated to check for the presence of prey in the stomach. As sea-kraits feed essentially on non-spiny fishes, it was easy to force them to regurgitate quickly their catch without risk of injury for the snake. On several occasions however, the preys were catfishes (*Plotosus lineatus*, see results), rendering this operation delicate; although still realisable with great care and patience (no snake was injured in these peculiar cases). On one occasion, the forced regurgitation provoked the death of the snake. Apparently the digested skull of a moray eel uncovered sharp teeth that probably cut a large blood vessel of

the snake followed by a fatal haemorrhage. Except this regrettable case, we never observed any trouble directly caused by forced regurgitation and many of the manipulated snakes were recaptured later. In order to minimise the stress associated with the loss of a large meal, we avoided collecting the stomach content on the same individual more than once. Similarly we discarded vitellogenic females and skinny snakes. The sampling bias hence introduced was partially compensated by spontaneous regurgitations and by a systematic collect of the preys during several weeks in 2005. We obtained 1,010 regurgitated prey items that were used for later identification. The preys collected were kept in 90% alcohol solution and identified to the nearest taxonomy level in the laboratory depending upon the state of the prey (i.e. presence of the dentition).

2.4 Reproduction

The abdomen of adult females was carefully palpated to detect and count growing follicles and/or ovulated eggs. Well developed follicles still in the ovaries or ovulated eggs in the oviducts are easily recognisable at palpation; notably the seconds are more mobile. We also observed courtship behaviour (jerking, intensive tongue flicking…) and mating with intromission of one of the hemipenises in the cloaca of the female on various occasions for both species. The timing of reproduction was inferred from those data. Laying periods were deducted from the comparisons between the periods during which vitellogenic females with large follicles or ovulated eggs have been observed and during which post laying females were detected. The post laying females were identified using recaptures (e.g. a vitellogenic female being recaptured with an empty abdomen) or after the inspection of the posterior part of the body: very emaciated females with a very distended skin revealing a recent laying episode.

3 Results and discussion

3.1 Colour pattern

Both species exhibit important variations; however the precise parts concerned by the variations (rings, background colour, and back versus belly for instance) diverge between the two species.

L. laticaudata – Although the typical colouration is banded pattern of regularly spaced black rings on a blue background (picture 1) our large sample size enabled to detect several cases of melanism (picture 1) and a relatively high proportion of incomplete or divided black rings. The blue background is weakly variable and ranged from light to dark blue. The period previous sloughing provokes a change in the blue colour, from a bright blue to a light (milky) blue. The total (body + tail) number of rings is highly variable, ranging from 35 to 55. Such values extend the previously documented patterns (from 36 to 44: Ineich et Laboute 2002, Saint Girons 1964 figure 2). The coloration tends to evolve with age as many large (presumably old) individuals present a dark (blackish) back with a fusion of the rings sometimes forming a line above the back spine (Lorioux et al. 2007). However melanic and melanistic individuals appear at low frequency. We observed one fully melanic male (absolutely black) and five melanistic individuals where the chin, or a small proportion of the belly where clear; All these six animals were large (> 1m in snout vent length). Melanism is assumed to take place during the juvenile phase. In the sea kraits, such changes can occur during adulthood. We observed a rapid colour change, a marked specimen shifted from a "normal" blue coloration to a melanistic phase in 9 months (Lorioux et al. 2007). The black rings were almost entirely fused in a general black background. The background colour of the belly is generally clear (whitish). Most of the individuals present white dots on the ventral part of the black bands and/or black dots on the white ventral space between the rings. Sometimes

these black dots join the rings, forming a ventral black line. Although most of the dots (black or white) are situated in the mid body, the position is very variable making unique combinations for each individual (sometimes helpful for individual identification).

PICTURE 1 - *Some examples of colour variation in the two species of sea kraits. From the top of the picture : a rusted* L. saintgironsi*, a normal* L. saintgironsi*, a normal* L. laticaudata *and a melanic* L. laticaudata *(© XB).*

L. saintgironsi – This species is also characterised by a banded pattern (hence the name tricot rayé). The background colour is far more variable compared to L. laticaudata. It ranges from greyish to bright red, with light brown and orange individuals (picture 1). In the south of the area (around the île des pins) the background is sometimes blue-grey, leading to possible confusion between the two

species by many peoples (hence the occurrence of each species based on interviews becomes unreliable). Most of the individual exhibit a dark yellowish background colouration. Some individuals (mostly on Signal islet but also on Mba, Larégnère, Porc-Epic and Amédée) present a rusted coloration, the background appearing bright orange or red (picture 1). Interestingly, our mark-recapture study shows that this is a temporary coloration, disappearing suddenly after sloughing. A high proportion of rusted animals occurs on the Ever Prosperity wreck, suggesting that this place is used as a resting site during long periods; at least for the superficial layers of the skin to be deeply impregnated by the rust. Most of the snakes captured on the wreck are digesting or in the shedding process, preparing their slough (e.g. the eye is opaque) or actually loosing the superficial layers of the skin. Many slough skins are observed on the wreck. For unknown reason, a number of yellow sea kraits were spotted on the highest metallic structures of the wreck, therefore displaying surprising climber abilities (see Bonnet et al. 2005). Several blue sea kraits also visit the wreck, their blue background do not turn into obvious rusted colour and they remain all on the lowest levels of the old vessel. The snakes that rest on the wreck originate from distant islets, for instance Signal Island is distant from 20km (Figure 1.). Based on recaptures, our data show that sea kraits can travel over long distance: for instance individuals marked on signal islet have been recaptured on Amédée islet (Figure 1.). The yellow sea kraits present fewer black rings relative to *L. laticaudata*; and the number of rings is less variable ranging from 25 to 39 (Figure 2). We never observed any case of melanism in this species, and the colouration apparently does not change with age (at least not in an obvious manner as observed in the blue sea krait). The belly is clear (whitish) and most of the individuals present some black dots between the black bands. The size of these white dots sometimes interrupt the black ring ventrally.

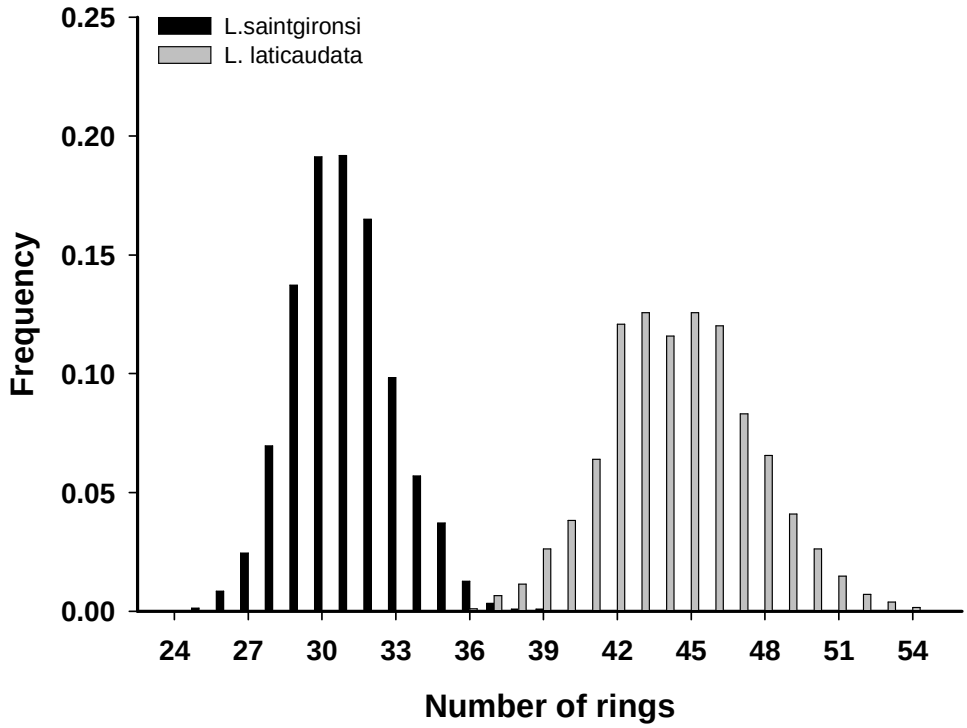

FIG. 2 - *Distribution of black ring number for* L. saintgironsi *(black) and for* L. laticaudata *(grey).*

Interestingly, some of the characteristics used to discriminate *L. frontalis* (a closely related species occurring in Vanuatu and the Loyalty Islands) from *L. saintgironsi* (Cogger and Heatwole 2006) are actually shared by the two species. Notably, the absence of a lower lateral connection between the black ring of the head and the first black ring of the neck, assumed to be typical from *L. frontalis* has been regularly observed in *L. saintgironsi*. Similarly the interruption of the ventral parts of the black rings, essentially in the front portion of the body, was commonly observed in *L. saintgironsi*. Interestingly, although observed in all our study sites, these problematic traits were very common in the south part of the lagoon (Bayonnaise and Brosse islets). This suggests that the boundary between *L. frontalis* and *L. saintgironsi*, in terms of colouration, tends to be particularly unclear in the

areas where the two species are the most likely to meet: Bayonnaise and Brosse islets are both relatively close to the Loyalty islands. Further studies are necessary to determine to what extent the two species are inter related through a gradient or are clearly separated through mating system frontier for example as demonstrated in the case of the closely related *L. colubrina* and *L. frontalis* (Shine et al. 2002a).

In both species, we observed incomplete or divided black rings. The most widespread anomalies are the half rings, the z-shaped and the y-shaped rings, they can occur either on the right or the left side of the snake. Other anomalies occur at a lower frequency: totally or partly fused rings (the y-shaped ring could be assimilated to a fusion between half and z-shaped rings), either on the back or the belly, a succession of thin and large rings instead of the regularly spaced rings, etc… We observed an individual with a belly with almost no ring visible. The bands were replaced by a succession of black squares (somewhat similar to the belly of *Natrix natrix*), the occurrence of y-shaped rings on the back was very high. All these peculiarities reinforce the confidence during individual identification.

3.2 Body size

The ranges of body sizes of the two species are given in the Figure 3.

L. laticaudata – relative to *L. saintgironsi*, the blue sea krait is a slender species that also attains larger size (Figure 3). The largest body size, 149cm for total body length (137cm SVL), was recorded on a female. This is a greater value compared to the other published maximal sizes for the species: 136cm total length by Greer (1997); 96cm SVL by Heatwhole (1999), and 108.7cm total length by Ineich and Laboute (2002).

L. saintgironsi – It is a medium sized, heavy bodied snake which makes it an intermediate sized species in the *L. colubrina* complex (in between *L. frontalis* and *L. colubrina*). The maximum SVL recorded for *L. saintgironsi* was 131cm total length (120cm SVL; Figure 3). This value is greater than the maximum body size of 109cm SVL provided by Cogger and Heatwhole (2006), but slightly smaller than a

specimen of 135.8cm total length examined by Ineich & Laboute (2002,). The fact that *L. saintgironsi* is more heavy built compared to *L. laticaudata* has been examined by Bonnet et al. (2005). The yellow sea snake is also relatively stronger as measured in terms of pulling-strength corrected by body mass (Bonnet et al. 2005), suggesting that the proportion of muscles is greater in this later species.

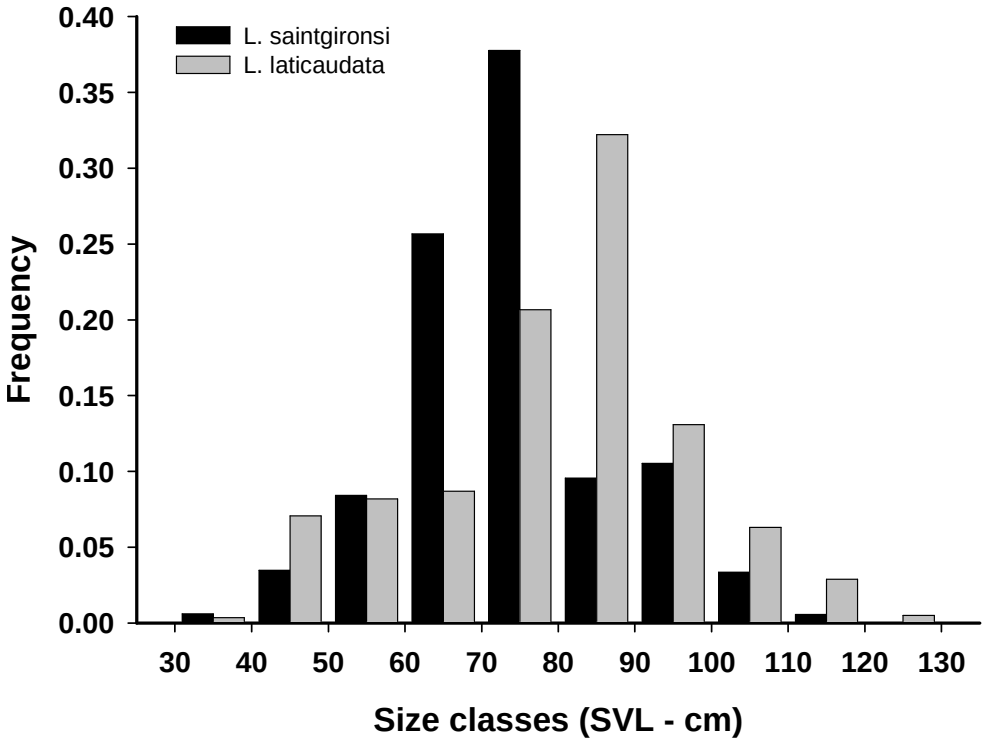

FIG. 3 - *Distribution of body length (SVL, cm) for* L. saintgironsi *(black) and for* L. laticaudata *(grey).*

3.3 Diet

Accordingly to other studies, *L. saintgironsi* is highly specialized on anguilliform fishes, 100% of the prey were moray eels or fishes with a similar gross morphology (anguilliform fishes, Shetty & Shine 2002d; Heatwhole 1999; Ineich & laboute 2002;

Reed *et al*. 2002). *L. laticaudata*, is often described as a snake that feed regularly on non-anguilliform fishes in the literature (Greer 1997; Heatwhole 1999, Ineich & Laboute 2002). Our data provide a different picture to this widespread view; the diet of the blue sea krait was constituted by 96% of anguilliform fishes in New Caledonia. We nonetheless found several non-anguilliform fishes, *Ptereleotris* sp., *Plotosus lineatus* and an unidentified species. The discrepancy between previously published data and our findings is probably due to the fact that our observations are based on a large data set compared to several anecdotic observations recorded under water.

The list of the species consumed by the sea kraits is provided in the Table 1. Such diversity of preys is likely among the most important in comparison with all the other species of snakes. As suggested in Vanuatu by Reed *et al*. (2002), sea kraits are extremely efficient natural samplers of the anguilliform fish communities. In New Caledonia, the analyses of the stomach content of the two species of sea kraits show that the anguilliform fish community was far more abundant and diverse than previously suspected (Ineich *et al*. 2007; Table 1). Through the snake's diet, we recorded 15 new fish species for the area. Studying the diet of the two neo-caledonian sea kraits offer enormous potential for monitoring the fish biodiversity of the lagoon, and to better understand how the species, and within species the sexes exploit the feeding resources. Notably to appreciate to which extend the species and the sexes compete or not during foraging activities.

TABLE 1 - *List of the fish species identified from sea kraits stomach contents.*

Family	**Species**
Muraenidae	*Anarchias allardicei*
	Anarchias sp.
	Cirrimaxilla formosa
	Echidna sp.
	Echidna unicolor
	Enchelycore pardalis
	Gymnothorax australicola
	G. albimarginatus
	G. buroenis
	G. chilospilus
	G. cribroris
	G. dorsalis
	G. eurostus
	G. favagineus
	G. fimbriatus
	G. fuscomaculatus
	G. gracilicauda
	G. meleagris
	G. moluccensis
	G. monochorous
	G. margaritophorus
	G. nudivomer
	G. pindae
	G. pseudothyrsoideus
	G. reevesi
	G. reticularis
	G. richardsoni
	Gymnothorax sp.
	G. undulatus

Family	Species
Muraenidae	*G. zonipectis*
	Scuticaria tigrina
	Scuticaria okinawae
	Stophidon sathete
	Uropterygius alboguttatus
	U. concolor
	U. fuscoguttatus
	U. macrocephalus
	Uropterygius sp.
	U. cf. xanthospilus
Ophichthidae	*Muraenichtys sp.*
	Myrophis microchir
	Myrichtys maculosus
	Ophichthus sp.
	Schismorhynchus labialis
Congridae	*Conger cinereus*
Muraenesocidae	*Muraenesox cinereus*
Microdesmidae	*Ptereleotris sp.*
Plotosidae	*Plotosus lineatus*

3.4 Reproduction

The few data available on the reproduction of the neo-caledonian sea kraits were incorrect. Therefore, the information presented below, although limited, provide the first basis that clearly show divergences between the two species.

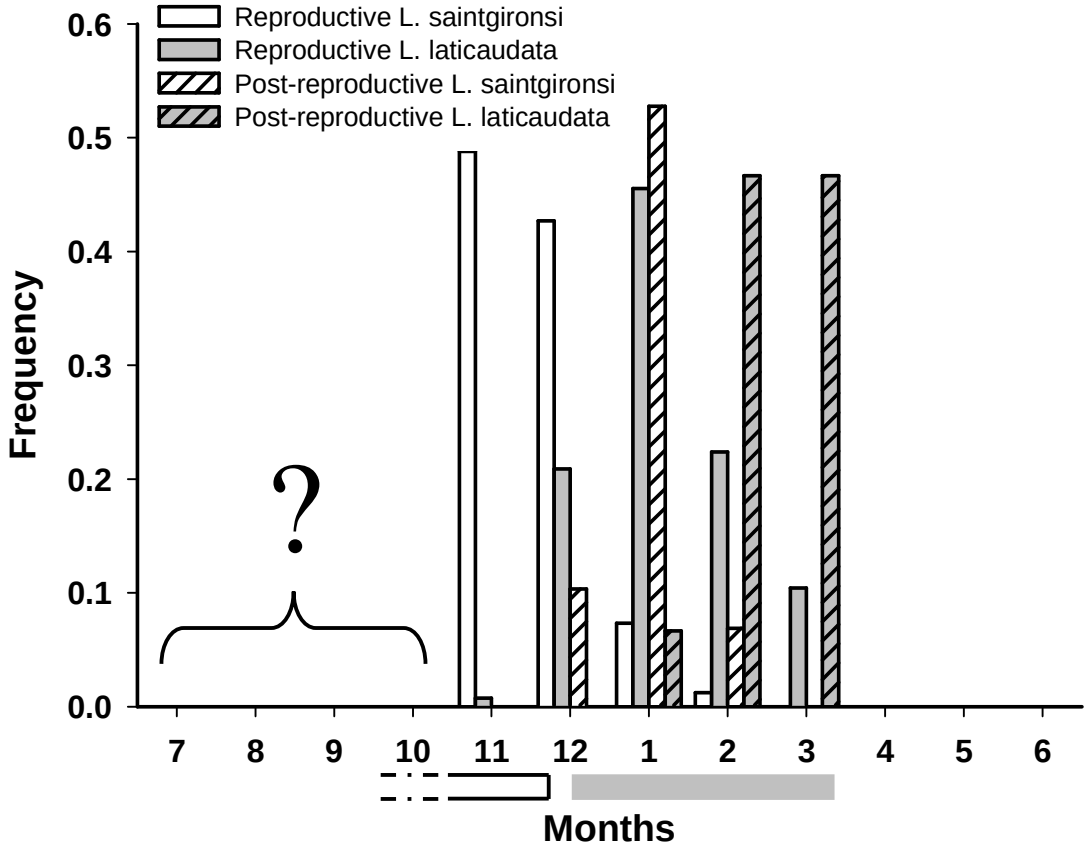

FIG. 4 - *Reproductive periods of sea kraits in New Caledonia. The white and grey boxes on the "Y" axis represents periods where courtship behaviour has been observed for* L. saintgironsi *and* L. laticaudata *respectively. The question mark represent period where no field work occurred.*

The presence of follicles and/or eggs in the abdomen of the females combined with the time during which we observed females with a very emaciated posterior part of the body, and courtship or mating enabled to characterize the timing of reproduction in both species (Figure 4). For *L. saintgironsi*, courtship and mating were observed in November (Figure 4). Unfortunately, our field work never began before November; it is likely that we missed the beginning of the mating period (Figure 4). Vitellogenic females were detected from November to February with a

peak in November-December. A three-four month period for vitellogenesis is a normal value in snakes, and thus was expected (Bonnet et al. 1994); however we cannot exclude the fact that the process might start earlier in October. Notably, our estimate for the duration of vitellogenesis may contain different cohorts of females; several starting earlier (October or before?) and the other later (December). Post reproductive females were detectable from December to late February with a peak in January, suggesting that the laying period ranged from December to February (Figure 4). For *L. laticaudata*, courtship or mating where observed much later, from early December to mid-March (Figure 4). Similarly, growing follicles or eggs were detected between December and March with a peak in January (Figure 4). The presence of post-reproductive females from January to March suggests that the laying period ranges from January to March (Figure 4). If so, this means that vitellogenesis may sometimes require only two month (Figure 4); reinforcing the notion that the females are not highly synchronised in the timing of reproduction. Overall, the respective reproductive period of the two species of sea kraits differ. Broadly *L. saintgironsi* breed earlier (last months of the year) compared to *L. laticauda* that breed essentially at the beginning of the year. Nonetheless, there is some overlapping between the two reproductive seasons from November to February (Figure 4).

The two species diverge for other reproductive characteristics. For instance in terms of behaviour during courtship or mating. *L. saintgironsi* was always observed in couple while *L. laticaudata* was always found in larger group with at least 2 males and up to 5 males attempting copulation. Courtship and mating was observed under large rocks or logs on a dry substrate in *L. saintgironsi*. By contrast, amorous *L. Laticaudata* were observed very close to the sea (partly under water), on a wet substrate and sometimes in the open (but at night). In both species we never observed male to male combat and the typical jerking of the male was displayed at a very low intensity compared to what can be observed in terrestrial snakes.

Meristic data on the size of the reproductive females and on clutch size are summarized in the Table 2. The smallest (presumably youngest) reproductive females attained 75.5cm in SVL in *L. saintgironsi* and 88.5 in *L. laticaudata*. These body sizes correspond broadly to the minimal size at maturity. For both species, clutch sizes are far smaller than previously stated (Saint Girons 1964, Ineich & Laboute 2002, Heatwhole 1999). For example, Saint Girons (1964) inferred from dissection and palpation that a clutch size of 15 eggs might be a minimal value for *L. saintgironsi*. We obtained a 5 times smaller value with a mean clutch size of 3 eggs (Table 2). However, Saint Girons did not had at its disposal fully vitellogenic females, and its count might be more related to the initial number of follicles recruited (or ready to be recruited) rather than to the actual number of follicles that will develop until ovulation stage. The data we provide for *L. laticaudata* are likely to be the first available for the area.

TABLE 2 - *Meristic data on reproductive female* L. saintgironsi *and* L. laticaudata.

	L. saintgironsi	***L. laticaudata***
SVL (cm)	92.08±7.56 (75.5-107.5)	107.28±7.94 (88.5-129.5)
N	80	102
Clutch size	3.25±1.27 (1-8)	3.61±0.88 (1-5)
N	72	90

Although the clutch size of the blue sea krait was slightly greater relative to the yellow sea krait, it was also less variable. As expected in a species were reproductive females are spread over a large range of body size (SVL from 75.5cm to 129.5cm pooling the two species) we found a positive correlation between maternal size and the number of follicles palpated (Figure 5).

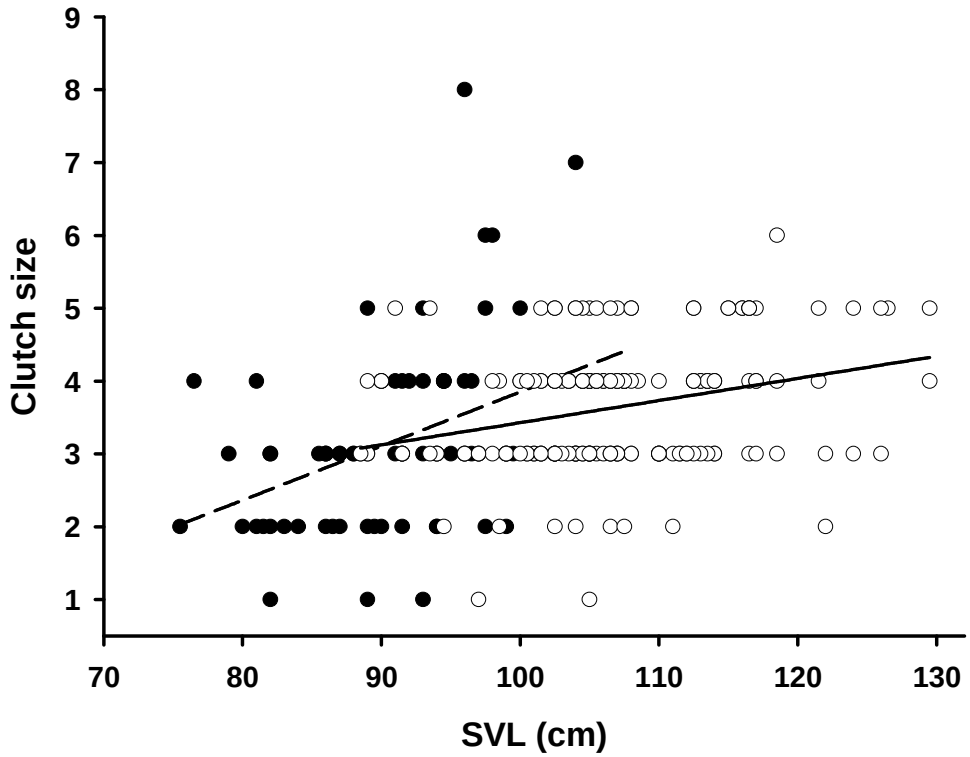

FIG. 5 - *Body length (SVL, cm) in relation to clutch size in* L. saintgironsi *(black circles) and* L. laticaudata *(white circles). SVL was positively correlated to clutch size in* L. saintgironsi *(dashed line, F=15.57, df=1.70, r²=0.18, p<0.001) and in* L. laticaudata *(black line, F=31.65, df=1.87, r²=0.27, p<0.001).*

Despite intensive field work during the putative laying period of both species, we still ignore where the females lay their eggs (and we thus still ignore incubation duration or embryonic stage at laying). Due to the configuration of the islets, the potential laying sites are not very diverse. The burrows of sea birds (Procelariforms) and the large block fields that are both intensively used as shelters by the sea kraits are the best laying sites identified yet. In the two places, the temperatures are stable and theoretically suitable for incubation (unpublished data). Although humidity is another crucial parameter we did not recorded accurately, the sand remained relatively wet in these two potential laying sites. As we never found any clutch deposited in its natural place, we also ignore the incubation time, and consequently

we have no accurate data on the neonates. A three-four month period is assumed to be reasonable (Guinea 1986). Given our large sample size, the smallest snakes observed likely provide a reliable estimate of the size of the neonates. The mean body size of the ten smallest sea kraits was 39.5±1cm (19±6g) in *L. laticaudata* and 37.5±2cm (21.5±7.5g) in *L. saintgironsi*. Such a relatively large size for the very young individuals corresponds probably to the minimal dimensions of the body and of the head necessary to catch and to swallow the smallest preys available to the neonates who also feed on anguilliform fishes.

In contrast to what has been stated, our information show that reproduction is very seasonal in New Caledonia for the sea kraits (Greer 1997). Most of the studies on the sea kraits have been carried out on equatorial populations. Geographic variations are likely to occur in the characteristics of reproduction accordingly to changes in environmental conditions (food availability, temperature, etc…). Our study populations are situated at the extreme south of the distribution range of the *Laticauda* genus. The winter is relatively cold in south New Caledonia. Perhaps that the ambient temperatures (of the water, air, and substrate) are not favourable to meet the physiological requirements of reproduction (i.e. high metabolic activity for vitellogenesis, mating, and incubation). In the same vein, perhaps that the high energetic and plastic demands of vitellogenesis are better covered in summer (high food availability, favourable temperature to catch and to digest the preys). Finally, the availability of small preys for the neonates might also be an important parameter that determines the seasonal character of reproduction of the sea krait. Teasing apart the respective contribution of these different factors will require an intensive field work.

3.5 Habitat

Broadly speaking, our numerous observations on the terrestrial habitats used by the neo-caledonian sea kraits are in accordance with the observation previously done by Saint Girons (1964). The snakes come on land to digest, slough their skin,

mate, rest, and lay their eggs. Most of the time they remain invisible to human observers. As typical snakes, they choose the roots of large trees, cavities, crevices, burrows, logs and large rocks to hide themselves. When the air is cool (e.g. <20°C), they can also be observed basking in the grass, or immobile in small puddles of hot water (>28°C) left by the tide on the flat beach rocks. As expected from sea snakes, the sea kraits tend to use mostly the habitats close to the shore. However, the yellow sea kraits sometimes undertake relatively long trips on land. *L. saintgironsi* notably tends to climb on the top of the hills (e.g. Porc Epic), on the trees and on any elevated structure that offers sufficient shelters. In comparison to *L. laticaudata*, this species is a better crawler and is an excellent rock climber (Bonnet et al. 2005). It also moves more frequently within the herbaceous vegetation that covers the inland, cruising during long periods, visiting different burrows. By contrast, the blue sea krait is never observed far from the sea. This species display poor abilities to move on land over long distances or to climb (Bonnet et al. 2005). Interestingly, it use intensively the large rock that are submerged at high tide.

To date, no extensive data is available about the submarine habitats used by the sea kraits (i.e. foraging areas). We do have relatively long (> 20hours) observations of the snakes foraging in the vicinity of the islet, exploring the coral matrix. However, this concerns solely the yellow sea kraits. All the blue sea kraits spotted under water were swimming in a strait direction toward or from the sea further than the reef flat. We know from the analyses of the stomach contents combined with numerous recaptures that the time spent at sea is devoted to foraging. We also know the spectrum of prey consumed by the snakes. However, as the ecology of the anguilliform fishes predated by the snakes is barely unknown, it is impossible to infer the foraging sites of sea snakes through their diet. We are currently setting up a study on diving behaviour.

3.6 Activity pattern

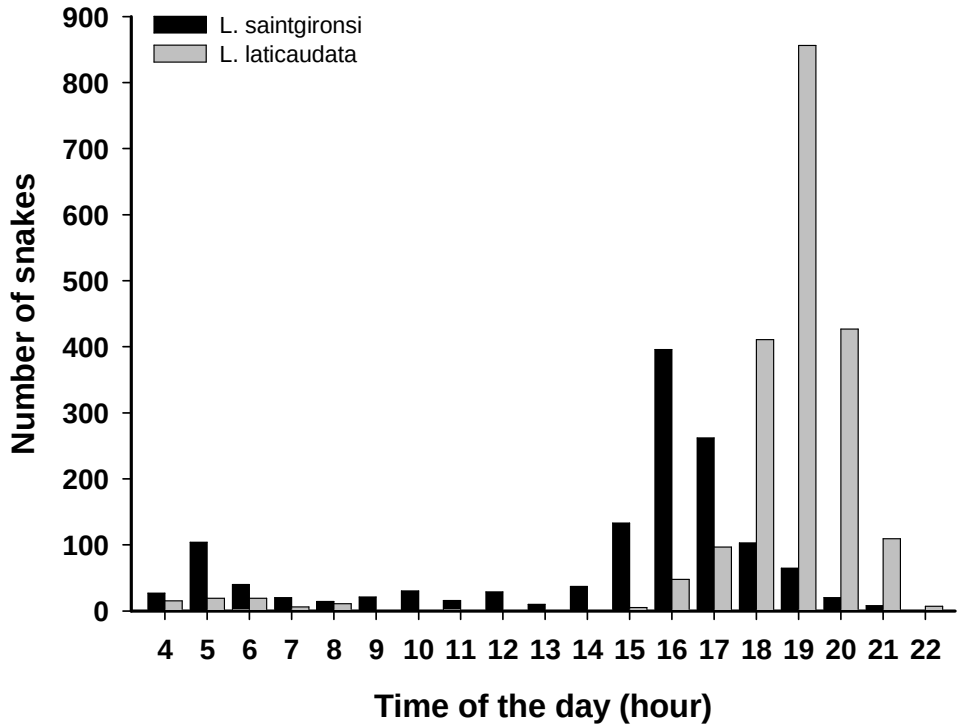

FIG. 6 - *Comparative pattern of catchability of* L. saintgironsi *(black bars) versus* L. laticaudata *(grey bars). Each bar represents the total number of snakes observed per-hour.*

Surprisingly, Saint Girons (1964) noticed that the sea kraits of New Caledonia do not exhibit any particular activity pattern. In contrast, our very first observations and our analyses revealed that the snakes decide to leave their shelters, to come on land, to mate or to swim parallel to the shore at very precise time periods. For example, there are sharp peaks of the locomotor activity displayed by the snakes with strong differences between the two species (Figure 6). *L. saintgironsi* began to move to or from the sea at the end of the afternoon (sunset) whereas *L. laticaudata* are mostly active after nightfall. This could be due to either predator avoidance or thermoregulation (to prevent overheating while crossing the beach).

When rain occur after a dry period, the usual activity pattern of snakes is disrupted. In these conditions, whatever the time of the day, the two species stop their usual activity to drink (Bonnet & Brischoux *submitted*).

3.7 Predators

Data on predation are scarce. The docile behaviour of sea kraits both on land and under water suggests that predation rates are low. Perhaps that the sea kraits rely on their spectacular banded pattern associated with potent venom as a main anti-predator tactic. A large fish was instantaneously killed after having swallowed a sea kraits (Aquarium of Nouméa, pers. com.). However, when on land the sea kraits flee away under the threat caused by rapidly approaching humans (Shine et al. 2003a); similarly, when moving under water a gentle touching of the snake triggers a fast swimming towards the nearest cavity in the coral. These behaviours reveal that the sea kraits still display the main anti-predator behaviour of most snake species. Clear predation cases are available on both habitats. On land, sea-eagles, and reef herons have been observed catching the snakes (Leach 1928, Bauer & Devaney 1987). Analyses of the stomach content of tiger sharks and of large cods indicate that the sea kraits are not excluded as food items by these large fishes (Rancurel & Intès 1982; Kulbicki com. pers.). Sea-anemone (Ineich & Laboute 2002; Devinck com. pers.), and crabs (Guinea, Voris & Jeffries in Heatwhole 1999) are able to capture juveniles and adult sea kraits as well (direct observations). Although important, all these information remain anecdotic and do not permit any quantitative evaluation of the impact of predation. Indirect data show that the conflict between the sea kraits and the fishes are quite common. The injuries (sometime impressive) and the scars that display many sea kraits (the majority of them in certain areas) reveal frequent attacks by fishes. The teeth marks and the jaw shape of the bite are easily recognisable. However, teasing-apart predation from defensive bites inflicted by potential preys is almost impossible. Indeed, it is likely that while prospecting for eels in the coral matrix, the coveted prey retaliate; moray eels notably are renewed

for their defensive abilities. Alternatively, the sea kraits might be attacked and sometimes consumed by the larger eels, some of them being largely out of their prey size range (> 1m). Predation on land is far more mysterious. During our intensive field work we never saw any capture or predation attempt by the birds supposedly dangerous to the snakes. Both reef herons and ospreys occur in large number in our study sites. One dead (mummified) sea krait has been found in an osprey nest (Signal Islet, 2003), but the skeleton of the snake was intact and the birds sometimes use strange items as nest ornamentation (P. Villard pers. com.). We acknowledge that our presence may deter the avian predators from trying to catch the snakes: indeed the birds are systematically threatened from relatively long distance by human walking on the beaches. Overall, the influence of the predators on the sea kraits is largely an open field.

3.8 Venom and bites

A common trait displayed by nearly all sea snakes (except the fish egg eater *Emydocephalus annulatus*) is a very potent venom that permits to kill the preys almost instantly. A very fast action of the venom might prevent the loss of the prey in the ocean; trailing a prey in such an environment might be very complicated for the snakes. Direct observations of sea kraits hunting moray eels confirm the extreme rapidity of the venom in killing the fishes. The venom of the sea krait is often described as one of the most dangerous, potentially lethal to the humans (Heatwole 1999; Ineich & Laboute 2002). However, these snakes are extremely docile; the occurrence of the bites to the humans is virtually equal to zero. Few cases of envenomations by sea snake have been recorded in New-Caledonia. Imprecise identification of the species of snake impedes to appreciate to what extent the sea kraits inflicted serious or fatal bites to humans.

In the course of our field study we manipulated thousands of snakes. Assuming that the snakes have been handled at least 3 times: at capture, during measurements and during releasing (we discard the many other manipulations, forced

regurgitation, locomotor performances tests…), we handled the snakes on more than 20,000 occasions. The vast majority of the snakes remained fully defenceless. A small proportion of them opened the mouth during handling. We experienced only 2 real defensive bites. Surprisingly, we noticed only moderate local and general troubles following the bites. It is impossible to state if the venom was injected in sufficient amounts to produce a strong effect. Greer (1997) noticed that bites are infrequent and are not considered dangerous to human. Overall the docile behaviour of the sea kraits is one of their prime traits in front of humans. Nonetheless, real bites are not fully impossible and the effects of a strong bite remain unknown. Therefore, the sea kraits must not be manipulated unless necessary.

3.9 Status of populations in New Caledonia

New Caledonia is one of the very rare spot on earth were very large numbers of venomous snakes cohabit successfully with human populations. The tricots rayés benefit from a positive image and most of the local peoples and tourists respect the snakes (although the snakes are very often considered are threatening creatures). The situation is not totally idyllic however as many sea kraits are still killed for totally unjustified reasons (Saint Girons 1964 and information below). Unfortunately, long term data are not available, rendering very delicate any attempt to assess the status of sea kraits. However, a number of examples permit to show that sea krait population can be negatively affected by human activities.

First, according to local peoples, the sea kraits were common on the 2 major beaches of Nouméa: Anse Vata and Baie des Citrons. Since 2002, despite intensive sampling, we never saw any sea kraits crossing these two sites. Few sea kraits can be observed under water nearby these beaches or resting in the sea water pumping room of the aquarium indicating that several individuals still cruise around. Both beaches have been completely modified to make them more attractive to the

tourists. Not the only the human frequentation is very high, but also all the potential shelters for the animals, rocks, or logs have been removed.

Second, on Maitre islet (near Nouméa), an officially classified natural reserve where hunting, plant collecting are prohibited, a recent construction of huge tourism infrastructure (how the permits were delivered is mysterious?) was preceded by the destruction of most of the natural islet on the side usually employed by the snakes (picture 2). The substrate, both on land and under water has been removed (sometimes using dynamite). Many buildings, concrete pathways, swimming pool, restaurant, bungalows etc. form a totally unsuitable habitat for the flora and the fauna. While the sea kraits were easily found until 2002, it is now barely impossible to observe any. The disappearing of the sea kraits was already obvious during the first stages of the destruction of the islet (observations by XB and II); strongly suggesting that the snakes have been actively killed in huge numbers to "clean" the area.

Last, on one of the surveyed islet (Konduyo, Figure 1), one of us (FB) failed to detect any sea krait. It was very surprising: the configuration of the islet apparently offered the same kind of environment than what is found on the other islets that accommodate high snake densities (e.g. Signal islet). We later learn that this islet has been inhabited during 25 years until recent years. We acknowledge that it is hard to know if a sea krait population existed before the presence of the humans but the total absence of snakes on that kind of islet led to some interrogations.

Hopefully, those cases are still limited, and most of the time the cohabitation of sea kraits and human is peaceful. Some of our study sites (Signal and Amédée islets for instance) support both high population density of sea snakes and a high human pressure with nearly hundreds of people visiting these <8 ha islets each week. Inevitably, most of the snakes have been closely approached by humans without being killed or injured. Although we still find regularly snakes crushed under rocks after the week-ends, obviously maliciously killed by human visitors, the mortality rate remains low and do not seem to impact the snake populations. It is likely that a

promotion in favour of the snakes could improve the situation. Many peoples and tourists are attracted by the sea kraits, perhaps thanks to their beautiful colour patterns. An effort of scientific vulgarisation about their natural history and ecology has been undertaken and should be developed.

PICTURE 2 - *Maitre islet, a natural reserve, during the construction of a huge tourism resort. The sign explain that it is forbidden to fish, capture, harvest or collect any animal or mineral; people must bring back their garbage; islet vegetation is fragile, it is forbidden to cut the trees; etc. It is still classified as a natural reserve ! (© XB).*

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Résumé du Chapitre

Ce chapitre est descriptif et pose les bases nécessaires pour avancer plus précisément dans l'exploration de l'écologie des tricots rayés de Nouvelle-Calédonie. L'examen de ces deux espèces a permis de décrire des facettes méconnues de leur écologie (ou de corriger des informations erronées).

Ce chapitre décrit les patterns de coloration, la morphologie, le régime alimentaire (au moins de manière générale), la reproduction, l'habitat terrestre et le rythme d'activité des deux espèces de tricots rayés de Nouvelle-Calédonie.

L'un des principaux résultat de ce travail montre que l'examen minutieux de ces deux espèces, présumées similaires, change complètement cette vision. En effet, *L. laticaudata* et *L. saintgironsi* exhibent des divergences profondes, quel que soit le paramètre examiné. En caricaturant, on pourrait dire que ces deux espèces de serpents n'ont en commun que leurs anneaux noirs (et encore, elles n'en n'ont pas le même nombre).

Néanmoins, ces descriptions restent en somme assez superficielles et il est évidemment nécessaire d'explorer comment ces différences se déclinent en détail. Pour cela, il est nécessaire d'examiner à part les activités ayant lieu dans les deux milieux de vie très contrastés utilisés par ces serpents : en mer et à terre.

Chapitre II

ECOLOGIE MARINE :
L'ACQUISITION DE NOURRITURE

COMPORTEMENT DE PLONGÉE

Snakes at sea:
diving performance of free-ranging sea kraits

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Abstract. Evolutionary transitions from terrestrial to marine life pose massive physiological challenges. Marine mammals and birds exhibit major adaptations of cardiovascular and respiratory physiology to increase the depths to which they can dive, and the time for which they can remain underwater. Marine reptiles have attracted far less attention in this respect, but we would expect ectotherms to outperform endotherms in several dive performances because ectothermy reduces oxygen demand. We surgically implanted dive-loggers in amphibious sea snakes (sea kraits, *Laticauda laticaudata* and *L. saintgironsi*) in the lagoon of New Caledonia, and recorded dive performance (e.g., depths, durations and post-dive intervals) for two free-ranging animals over periods of 8 and 11 weeks. During foraging excursions the snakes spent > 80% of their time underwater, diving > to 80 m and for periods of > 130 min. Inter-dive intervals were brief, typically < 45 sec, suggesting that dives were aerobic. Dive patterns in these animals differ in major respects from those of previously-studied marine endotherms, turtles and pelagic sea snakes.

1 INTRODUCTION

Evolutionary transitions in habitat use provide exceptionally powerful opportunities to understand the selective pressures operating on morphology, physiology and behaviour, especially if the novel habitat poses physical challenges different from those experienced in the ancestral habitat type. For example, aquatic life exerts major selection on attributes such as the ability to move efficiently through water, to remain underwater for long periods without needing to surface to breathe, and to dive to considerable depths (Kooyman, 1989). The morphological, physiological and behavioural attributes that facilitate such tasks are very different from those required in the day-to-day lives of most terrestrial organisms. Accordingly, lineages of terrestrial vertebrates that have evolved to exploit marine habitats provide many striking examples of adaptation to aquatic life (Boyd, 1997; Kooyman, 1989).

Some of the most clearcut examples of adaptation to marine life involve modifications of endothermic vertebrates (whales, seals, penguins, etc.) related to diving performance (Butler and Jones, 1997; Boyd, 1997). Notably, compared to their terrestrial homologues, diving endotherms are able to store large amounts of oxygen via abundant haemoglobin and myoglobin, and increased blood volume. They also reduce oxygen needs while diving by reliance on anaerobic metabolism, peripheral vasoconstriction, bradycardia, and decreased body temperature (Butler and Jones, 1997; Boyd, 1997). Likewise, cardiovascular adjustments and reinforcement of body cavities reduce susceptibility to the high hydrostatic pressures encountered at depth.

Despite these adaptations, air-breathing vertebrates are highly constrained in dive duration and depth. Prolonged dives inevitably increase plasma CO_2, levels and reduce oxygen stores; the resultant shift to anaerobic metabolism increases lactic acid concentration which in turn forces the animal to spend even longer periods of time resting at the surface after dives, breathing to purge its physiological debt (Butler and Jones, 1997). Although such issues are universal for air-breathers,

they should apply with much less force to ectotherms than to endotherms. Indeed, Pough's seminal (1980) review of the advantages of ectothermy identified the exploitation of underwater niches as a key adaptive zone available to ectotherms. First, the low metabolic rates of ectotherms (comparatively to endotherms) reduce oxygen needs, so that a given oxygen store can support the animal's activities for a much longer period. Second, at least in the tropics, because water temperatures are so high, thermal exchanges between animals and the surrounding water are not a limiting factor on snake metabolism. Accordingly, ectotherms escape the body-shape constraints associated with endothermy, and can exhibit high ratios of surface area to volume that in turn allow for high rates of oxygen uptake underwater across the body surface (Avolio et al., 2006).

These contrasts suggest that all else being equal, marine ectotherms should outperform endotherms in several aspects of dive performance. Hence, we expect to see that marine reptiles should exhibit longer, and potentially deeper dives, more leisurely rates of ascent and/or descent, and shorter post-dive intervals, than would be possible for marine endotherms. Available data are not adequate to test this prediction, because studies have focused strongly on endotherms whereas marine reptiles have attracted far less attention. The most detailed studies come from work with marine turtles (Eckert et al., 1989; Sakamoto et al., 1993; Southwood et al., 1999; Hochscheid and Wilson, 1999; Hochscheid et al., 1999, 2005; Hays et al., 2004; James et al. 2005). Surprisingly, marine turtles display maximum dive-depth and dive-duration values within the range of those observed in mammals and birds (Schreer and Kovacs, 1997). They are able to remain under water for long time periods when environmental temperatures are low (Butler and Jones, 1982), but animals in this situation are in torpor and virtually motionless. Similarly extended submergences have been recorded in inactive individuals not only in other species of reptiles (Andersen, 1961; Wood and Moberly, 1970; Wood and Johansen, 1974 Ultsch et al., 1999) but also in mammals (hippopotamus, Pocock, 1918 in Parker, 1935). Therefore, such dive durations cannot be compared directly with those of actively

foraging endothermic vertebrates (i.e., foraging diving must be clearly distinguished from torpor). Thus, for comparison with active aquatic endotherms, we need data on free-ranging ectothermic animals in the course of their daily foraging activities.

The recent development of miniature data loggers (Time-Depth Recorders, TDRs) has the potential to enormously facilitate such studies. Such units have clarified dive patterns in marine turtles (Eckert et al., 1989; Sakamoto et al., 1993; Southwood et al., 1999; Hochscheid and Wilson, 1999; Hochscheid et al., 1999, 2005; Hays et al., 2004; James et al., 2005) but as yet, have not been applied to the wide array of marine reptiles belonging to other lineages. Snakes are of particular interest in this regard, because aquatic habits have evolved independently in at least 4 separate phylogenetic lineages of these elongate animals (Heatwole, 1999). Two of those origins, in particular, have resulted in familial-level radiations of sea snakes: the Hydrophiidae (or "true sea snakes") and Laticaudidae (or "sea kraits"). The only sea snake from either lineage previously studied in detail with respect to dive performance is a hydrophiid, the pelagic *Pelamis platura* (Rubinoff et al., 1986). Although pioneering, these authors relied on externally-mounted transmitters that generated substantial drag on swimming snakes and had very limited memory. Furthermore, *P. platurus* displays unusual diving behaviour, in that it apparently dives to avoid surface currents rather than to feed, unlike all other sea snake species.

In this study, we investigated the diving behaviour of two species of sea kraits. The aim was to implant for the first time Time-Depth Recorders (TDRs) surgically on sea snakes in order to provide novel quantitative data on time-budget and diving behaviour.

2 MATERIAL AND METHODS

2.1 Study site and species

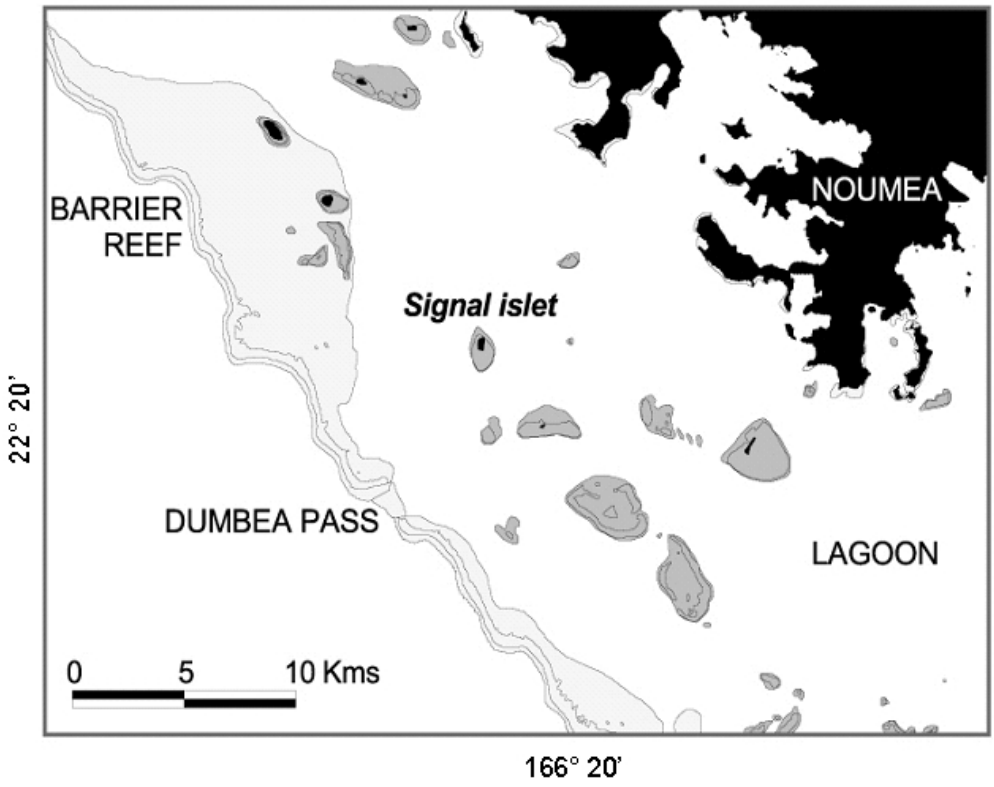

FIG. 1 - *Study area. Signal Island is situated in the SW lagoon of New Caledonia (22°17'46" S; 166°17'35" E). Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by the light grey areas.*

Fieldwork was conducted from December 2005 to March 2006 on Signal Island, a 6-hectare islet in the southwest lagoon of New Caledonia, 15 km west of Nouméa and 10 km from the external reef barrier (22°17'46" S; 166°17'35" E, Fig. 1). Sea-kraits are large (up to 1.5 metre) venomous snakes that forage in the ocean, mostly on anguilliform fishes, and return to land to digest their prey, mate, slough their

skins, and lay their eggs (Heatwole, 1999; Shetty and Shine, 2002b). Two species of sea kraits are broadly sympatric in New Caledonia: *Laticauda saintgironsi* (Cogger and Heatwole, 2006; formerly regarded as part of the wide-ranging *L. colubrina* Schneider 1799) and *L. laticaudata* (Linné 1758, [Saint Girons, 1964; Ineich and Laboute, 2002]).

2.2 Devices

A total of five sea kraits (1 male and 2 female *L. laticaudata*; 2 female *L. saintgironsi*) were captured on Signal Island and fitted with Time-Depth Recorders (TDR LTD-1110 data-loggers, Lotek Wireless Inc., Canada). As this was the first attempt to describe diving behaviour in sea snakes, we were unable to predict the parameters needed to program TDRs with the optimal sampling interval. For example, it was impossible to know how long it would take to the snakes to recover from surgery and undertake a new fishing trip, or when the snakes would be recaptured after fishing trips. We therefore programmed the TDRs to record data with a variable sampling interval: when the 32kb tag memory was filled, the sampling interval doubled, decreasing precision of diving parameters but retaining information on mean dive depth and duration of foraging trips and periods on land. Depth and temperature reading resolution was ±1 m and ±0.1 °C, respectively.

To facilitate relocation and recovery we also implanted a small radio-transmitter (SI 2; Holohil Systems Ltd., Canada) in each snake. The combined mass of the data-logger (11mm × 32mm, 2g) and transmitter (11mm x 33mm, 9g, with a 20 cm whip antenna) corresponded to 2 to 5% of the snake's body mass, in accordance with Kenward's (1987) recommendations. For comparison, we note that the transmitters used by Rubinoff et al. (1986) were slightly larger than our own (based on linear dimensions, they probably weighed about 6 to 8% of snake mass).

2.3 Surgery

Snakes were captured by hand while crossing the beach. There are no buildings on Signal Island, so surgery was conducted under shelter on a sterilized beachside table. Snakes were anaesthetised using isoflurane gas (Abbott Laboratories, Illinois, USA) administered through a mask; induction of anaesthesia required ~ 10 min. Surgical instruments were heat-sterilized and the animal's skin was disinfected with Bétadine©. Loggers and transmitters were cleaned with bleach and dried with sterile cloth prior to insertion. Snakes were incised laterally on the left side (to avoid a major midventral vein, and the lung which lies towards the right side of the body). The incision was made with surgical scissors just posterior to the stomach and the transmitter inserted first (the whip antenna was inserted under the skin towards the tail). The TDR was placed posterior to transmitter, with the pressure sensor facing the animal's tail. The 3-cm long incision was stitched with resorbable surgical thread (4 stitches per incision), and again disinfected with Bétadine©. Total duration of each operation was ~ 45 min. Snakes usually recovered from anaesthesia within 5 min of the cessation of surgery, and were then kept in calico bags and released after 48 hours of careful monitoring.

2.4 Tracking

We tracked the snakes with a directional antenna and an AVM LAQ12 receiver daily or more often during a 5-week period immediately following release, and then during a 2-week period 15 days later, in order to monitor behaviour and determine if and when snakes left the islet to forage at sea. Immediately after release, snakes stayed hidden under rocks or in bird burrows for a mean period of 27±7 days. After sloughing (direct observation of two snakes), the snakes began to alternate foraging trips at sea with periods on land (fig. 2A,B).

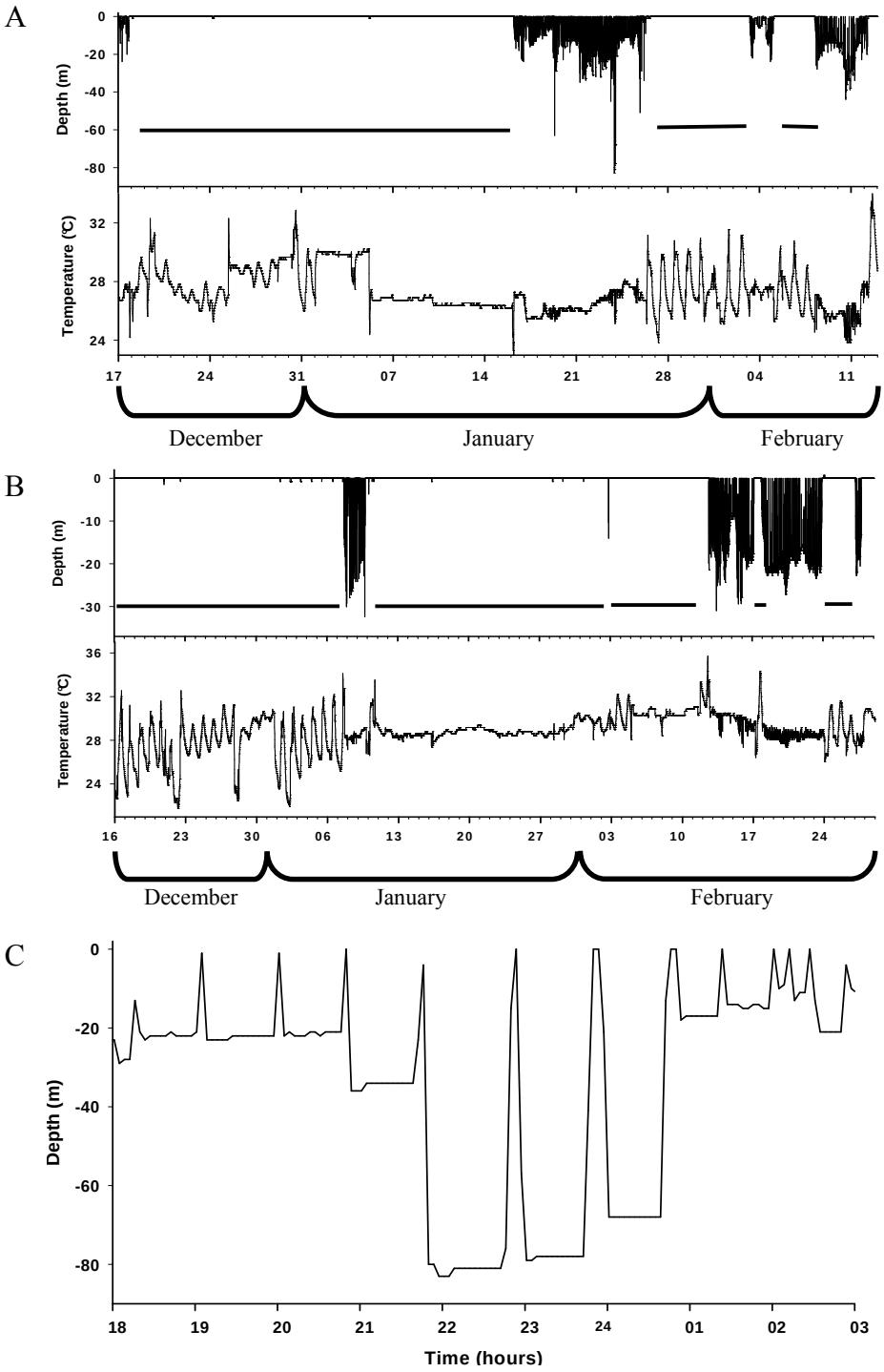
A
Depth (m)
0
-20
-40
-60
-80
Temperature (°C)
32
28
24
17
24
31
07
14
21
28
04
11
December
January
February
B
Depth (m)
0
-10
-20
-30
Temperature (°C)
36
32
28
24
16
23
30
06
13
20
27
03
10
17
24
December
January
February
C
Depth (m)
0
-20
-40
-60
-80
18
19
20
21
22
23
24
01
02
03
Time (hours)

FIG. 2 - *Examples of depth and temperature recordings by implanted data-loggers (A) for* L. saintgironsi *and (B) for* L. laticaudata. *Horizontal black lines correspond to time spent on land. Plot (C) provides a detailed view of deep dives for* L. saintgironsi *during the night between the 23rd and the 24th of January 2006. Interestingly, this profile is virtually the inverse of that seen in aquatic endotherms - if read upside-down, it resembles a classical endotherm dive profile, with short dives and long recovery periods.*

Three of the five snakes were recaptured 2 two 3 months after release, but one of these animals had remained on land for the entire intervening period. The remaining snakes (1 female *L. laticaudata* and 1 female *L. saintgironsi*) underwent foraging trips (confirmed by their absence from the islet, and by finding food inside one of these snakes when it returned) and hence provided useful data for the current analysis.

2.5 Data analysis

Most of our data had a long (450 sec) sampling interval, but we obtained more detailed (one sample per 225 sec) data on a 10-day foraging excursion by the female *L. saintgironsi*. Dive parameters for this fishing trip were analysed using Multitrace (Jensen Software Systems) to calculate dive depths, dive durations, and post dive intervals (PDIs) for all dives. Ascent and descent rates were calculated only for a single dive that presented enough data points during the ascent and the descent. Data from all other sampled fishing trips were used for trip duration estimates and time-at-depth analyses. Below, mean values are given ± standard deviations.

3 Results

3.1 Duration of aquatic and terrestrial activity phases

Post-recovery, fishing trips alternated with periods on land (Fig. 2A,B,C). Overall, foraging trips lasted an average of 3.70±3.31 days (range 0.05-10.14 days)

and periods on land averaged 7.04±8.25 days (range 0.64-24.00 days). While at sea, the two sea-kraits spent little time at the sea-surface (Fig. 3). Overall, during their aquatic life the snakes averaged 19% of time on the sea surface.

3.2 Depth profiles

Foraging snakes used a wide range of dive-depths, from 1 to 83 m. Of the two snakes studied, the *L. saintgironsi* tended to use both shallower and deeper water than did the *L. laticaudata*, which used intermediate depths (Fig. 3).

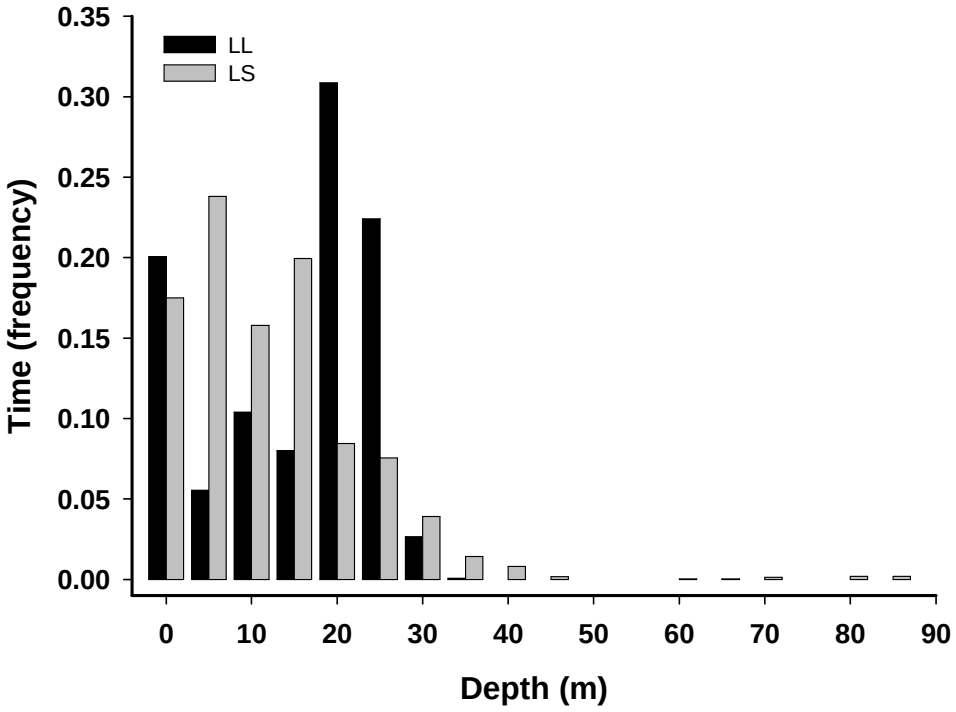

FIG. 3 - *Distribution of the time-at-depth profiles for two species of sea-kraits. Black and grey bars represent* Laticauda saintgironsi *and* L. laticaudata *respectively. Maximum dive depth was 83 m for* L. saintgironsi *and 32 m for* L. laticaudata.

3.3 Detailed analysis of foraging trip by *L. saintgironsi*

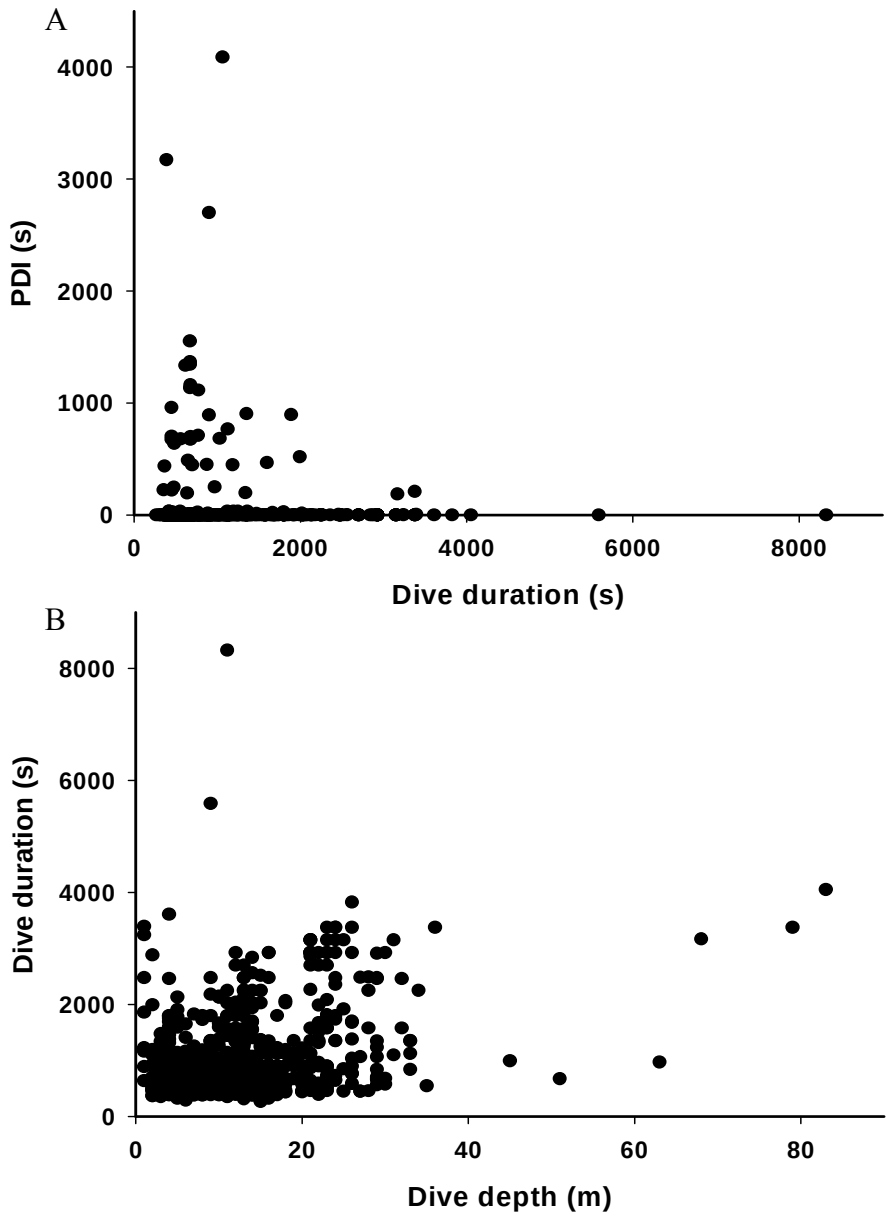

FIG. 4 - *(A) Post dive interval (PDI) in relation to dive duration, and (B) dive duration in relation to dive depth for the sea krait* L. saintgironsi.

During this 10-day trip, the snake dove 833 times (84.1±18.1 dives/day). Those dives occurred both during the day (525 dives, ~ 4 dives/hour) and at night (308 dives, ~ 3 dives/hour; χ^2=56.53,dl=1, p<0.001). Overall dive depth averaged 12±8 m, with a range of 1 to 83 m. Most dives were < 30 m (Fig. 3), and during the course of a single dive the snake tended to remain at the same depth throughout its foraging period (Fig. 2C). Mean depths were similar for diurnal dives (12±7 m) versus nocturnal dives (12±10 m; t-test, p=0.32). Dive duration averaged 16±12 min (range 4 to 138 min) and averaged slightly longer by night than by day (20±16 vs. 14±10; t-test, p<0.001). Periods spent at the sea surface between dives were remarkably brief, averaging 0.7±4min (<225 sec to 68 min) and affected only slightly by time of day (diurnal mean 0.5±2.5, nocturnal mean 1±6 min; t-test, p=0.04). Ascent and descent rates calculated on one dive were relatively slow and gradual (0.26 m/sec for both rates).

The duration of the post-dive interval was not correlated with prior dive duration (Fig. 4A), but we detected a weak but statistically significant correlation between dive duration and dive depth (F=115.9, df=1.8, r^2=0.12, p<0.001, Fig. 4B). The temperature range experienced by the snake during a dive tended to decrease with depth, but the trend was not statistically significant (F=1.19, df=1, r^2=0.08, p=0.29, Fig. 5).

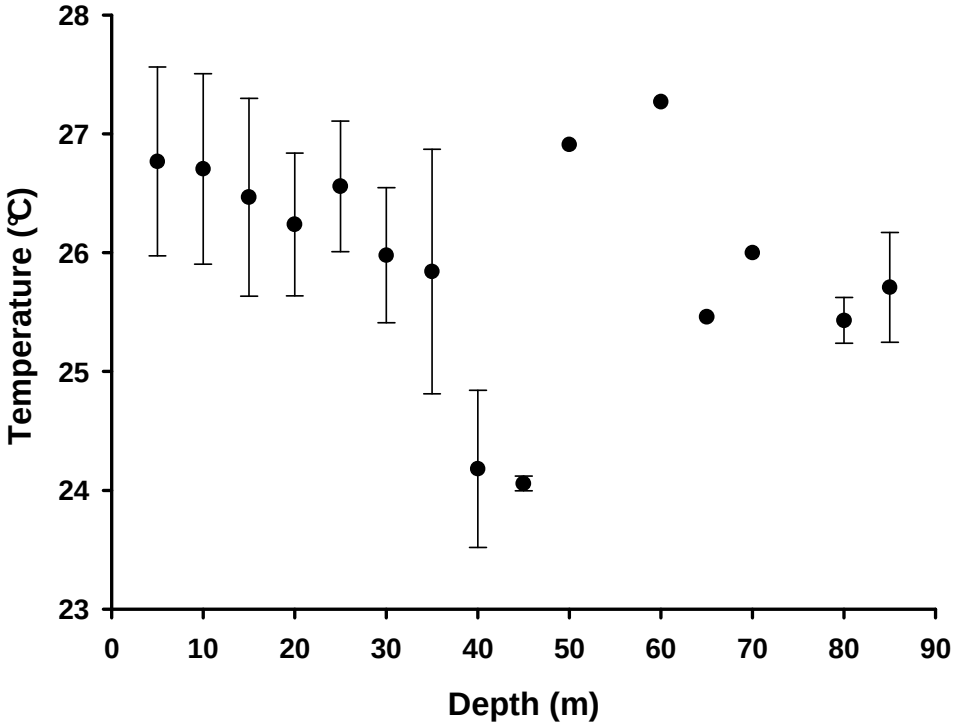

FIG. 5 - *Body temperature (mean ± SD) in relation to dive depth experienced by the sea krait* L. saintgironsi.

3.4 Diving performance relative to previously-studied species

The extensive data available for marine endotherms and turtles provide an interesting comparison with our results for sea kraits. Perhaps the most consistent pattern emerging from the published literature is the relationship between body mass and maximum dive duration: larger animals can stay underwater for longer (Schreer and Kovacs, 1997; Halsey et al., 2006; Fig. 6A). As predicted (see Introduction), ectotherms exhibit greater maximal dive durations than do

endotherms of comparable body mass. Maximum dive depths on the other hand, are similar to the depths reached by foraging sea birds (fig 6B).

All of the sea snakes for which we have data (present study, Heatwole, 1975; Rubinoff et al., 1986; Fig. 6A,B) exhibit dive durations unachievable by endotherms < 100 kg (Fig. 6A). For most of these species, dive duration data were obtained by direct observations, and probably do not represent physiologically maximal dive durations for the species involved (Heatwole 1975). Nevertheless, for the two species for which we have continuous recording over a large number of dives, the superiority in dive performance over endotherms is spectacular: both *Pelamis platurus* (mean 137 g, Rubinoff et al. 1986) and *Laticauda saintgironsi* (390 g, present study), exhibited dive durations unachievable by endotherms < 600 kg (Fig. 6A).

4 Discussion

4.1 The method

Despite a limited sample size in terms of numbers of individual animals, our study provides the most extensive data set available in terms of numbers of dives and detail of depths, durations and post-dive intervals for free-ranging sea snakes. Indeed, a total of 833 dives over 10 days were recorded for *L. saintgironsi* alone. Recent technological developments allow detailed monitoring of such traits in free-ranging animals, in circumstances that provide much more detail than is possible with visual observation alone (e.g., Heatwole 1975) and that minimize experimental artefacts associated with earlier technologies (e.g., Rubinoff et al. 1986). Intraperitoneal implantation of devices (radio-transmitters and temperature loggers) is now routinely used to study the ecology of terrestrial snakes (Reinert and Cundall, 1982), and clearly can work well with aquatic species also.

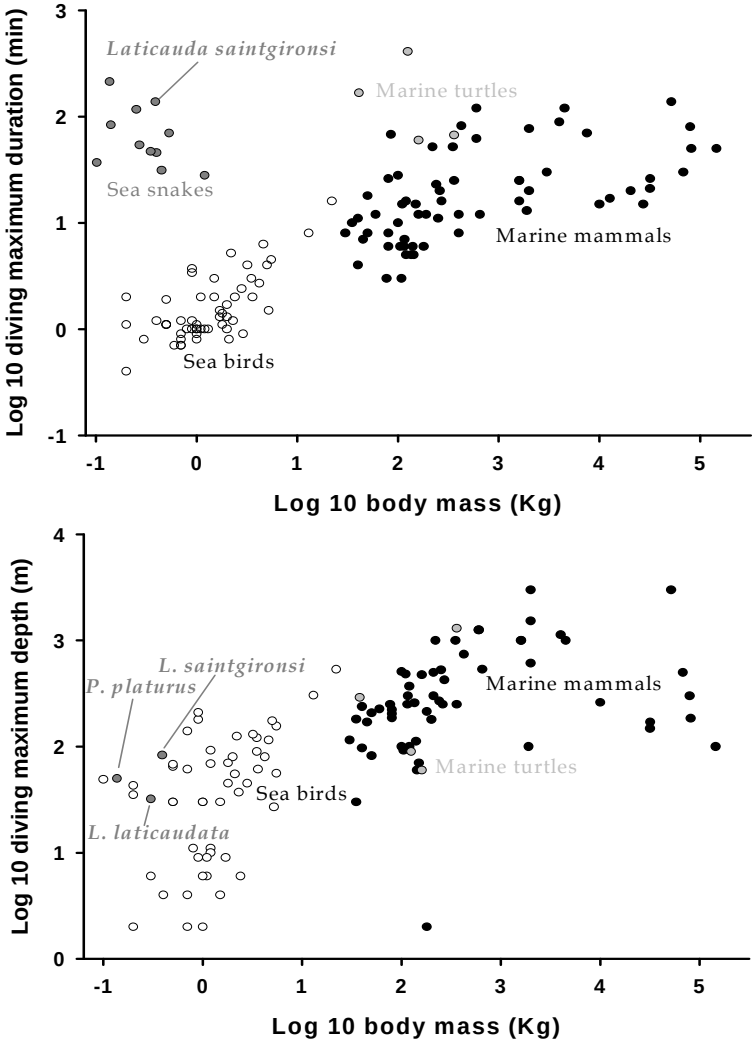

FIG. 6 - *Allometric relationship between body mass and maximum dive duration (A) and maximum dive depth (B) in several species of air-breathing diving vertebrates. For sea birds (open circles), marine mammals (black circles) and marine turtles (light grey circles), data on body mass (kg), maximum dive duration (min) and maximum dive depth (m) were gathered from Schreer and Kovacs 1997. We updated the data on marine turtles with recent studies (*Dermochelys coriacea *Southwood et al. 1999,* Caretta caretta *Hochscheid et al. 2005,* Chelonias mydas *Hays et al. 2004). For sea snakes (dark grey circles), we used data from the present study (depth and duration for* L. saintgironsi*, depth only for* L. laticaudata*) and the data available in the literature (duration and depth for* Pelamis platurus*, Rubinoff et al. 1986; duration only for nine other species of sea snakes, Heatwole 1975).*

Implantation of TDRs in sea-kraits enabled us to gather the first automatically recorded data on the diving behaviour and activity budget of sea snakes. Concurrent data on depth and temperature allowed us to robustly distinguish time spent at sea *versus* on land. The devices were deployed for periods of 2 to 3 months, and recaptured snakes appeared healthy and unaffected by the experimental procedures. Nevertheless, our implanted snakes spent a long time on land post-surgery, as did the closely related species *L. colubrina* after being exposed to similar procedures (mean 22.8 days, Shetty & Shine 2002b). After sloughing, however, the snakes resumed their usual activities. After recovery, durations of time spent at sea *versus* on land were consistent with previous data based on radio-tracking (Shetty & Shine 2002b) and from mark-recapture (unpublished data). This similarity suggests that TDR implantation used in did not affect negatively sea-snake behaviour. Similarly, the recapture of one individual with food in its stomach suggests that feeding was not impeded by the presence of the TDR in the body cavity.

4.2 Diving behaviour of sea kraits

In respect of variables that can be directly compared between our study and earlier work on diving in sea snakes, there are both important similarities and differences. For the variable most extensively documented (dive duration), all sea snakes so far studied show consistent dive performance, massively greater than achievable by endothermic marine animals (Fig. 6A). The tight clustering of sea snake data in Figure 6A is especially impressive in that the species involved belong to three separate lineages that have independently made the transition from terrestrial to aquatic habits (acrochordids, hydrophiids, laticaudids). Although data for other variables are less extensive, sea snakes also appear to exhibit relatively similar abilities in terms of maximal dive depths (Fig. 6B).

One extensive data series from a dive-logger paints a clear picture of a foraging trip by a laticaudid sea snake, and shows several novel patterns (Figs. 2A,C, 4). First, the snake was active very consistently over a prolonged period, in strong contrast to the episodic (and often, infrequent) activity of foraging terrestrial snakes (Greene, 1997; Shine et al., 2004a). Indeed, sea kraits appear to be extremely active animals, spending weeks at a time in dive after dive, 24 hours a day, without any resting period. Interestingly, a hydrophiid sea snake using a very different prey resource (*Emydocephalus annulatus* foraging for fish eggs) also shows virtually non-stop motion during each foraging bout (Shine et al., 2004a); the low cost of aquatic locomotion (due to buoyancy) may facilitate such continued activity.

Second, a typical dive involved a gradual ascent and descent separated by a relatively long period (> 55 % of total dive duration) during which the snake remained at an approximately constant depth (Fig. 2C). Our visual observations of foraging *L. saintgironsi* show that these periods are devoted to moving along the coral substrate, exploring holes in the matrix and tongue-flicking in an apparent search for prey items (anguilliform fishes). The bathymetry of the New Caledonian lagoon accords well with this interpretation, because the range of depths in sites near Signal Islet is similar to the depths at which our study organisms spent most of their time during foraging trips (SHOM website, http://www.shom.fr).

Third, post-dive intervals were remarkably brief (typically, < 45 sec) and unrelated to duration of the prior dive (Fig. 4A), showing that even these prolonged dives were sustainable without resorting to anaerobic metabolism. Fourth, the leisurely rates of ascent and descent (ca. 32% of the snakes' maximum swimming speed of 0.8 $m.s^{-1}$, Shine et al., 2003b) accord with the lack of any strong physiological constraint on dive duration. This poses a strong contrast to the rapid ascent and descent rates of endothermic marine animals; for example, mean swimming speeds were 71% of maximum swimming speeds in Adélie penguins (Yoda et al., 1999), 45% in king penguins (Culik et al., 1996), 82% in California sea lions (Feldkamp, 1987) and 67% in New Zealand sea lions (Crocker et al., 2001).

Interestingly, New Zealand sea lions accelerate (mean descent speed 148% of mean surface swimming speed) during ascent and descent to decrease transit time and thus increase bottom time or depth. The great lability in metabolic rates conferred by ectothermy means that sea kraits can achieve the same result (increased dive duration and thus, time available to explore the bottom) by adopting low swimming speeds that reduce rates of oxygen consumption.

4.3 Comparison with previous studies

The only detailed data on snakes with which we can compare our results come from Rubinoff et al.'s (1986) pioneering study of the pelagic sea snake *Pelamis platurus* in deep oceanic waters of the Gulf of Panama. Using externally-attached ultrasonic transmitters, these authors quantified dive times and depths. Despite broad similarities in some aspects (maximum dive depths and durations, post-dive intervals), several differences are apparent also. Most notably, *P. platurus* dove near-vertically (typically to around 15 m) and then immediately began ascending very slowly (ascent many times slower than descent: Rubinoff et al., 1986), whereas *L. saintgironsi* dove slowly, remained at a constant depth while foraging, then ascended at about the same rate as it had descended (Fig. 2C). This difference presumably relates to the different functions of diving in the two species. *Pelamis platurus* feeds only at the sea surface, and dives primarily to avoid surface currents and thereby control its position; slow ascent may allow the snake to locate potential feeding sites (slicks, etc.) and move up into them (Rubinoff et al., 1986). In contrast, *L. saintgironsi* searches actively for its anguilliform prey among the coral matrix (Heatwole, 1999; Reed et al., 2002; Ineich et al. unpublished), and spends most of the dive cruising close to the sea bottom in chemosensory exploration of crevices that might contain eels (pers. obs.). In this respect, the dive profiles of laticaudids are likely to be more typical of other sea snakes (many of which take fishes from the coral matrix) than is the "quick dive-slow ascent" pattern documented for Rubinoff et al. (1986) for *P. platurus*. Similarly, the purely benthic U-shaped dives of *L.*

saintgironsi and *L. laticaudata* compared to the pelagic dives of *P. platurus* reflect the need for the former species to reach the sea floor whereas the latter taxon needs to dive only deep enough to avoid surface currents.

Previous studies on dive performance in marine mammals and birds have emphasised the magnitude of physiological challenges faced by these animals, and the degree to which multiple adaptive shifts have enhanced performance compared to their terrestrial counterparts (Kooyman, 1989; Boyd, 1997). Analysis of dive performance in sea snakes generates a very different perspective. First, these animals do not show such dramatic modifications associated with aquatic life. Except for an increase in lung volume and in skin oxygen absorption abilities, they broadly resemble their terrestrial relatives (Heatwole and Seymour, 1975; Graham, 1974; Belkin, 1963). Nonetheless, these snakes massively outperform endotherms in terms of dive performance, with a 150 - 400g snake able to dive for at least as long as a 600 kg elephant seal (Fig. 6A). These comparisons strongly support the hypothesis that ectothermy preadapts reptiles to exploit underwater resources in tropical oceans, because reduced or lack of access to oxygen poses much less of a physiological challenge to these animals than it does to endothermic taxa attempting to utilise the same environments.

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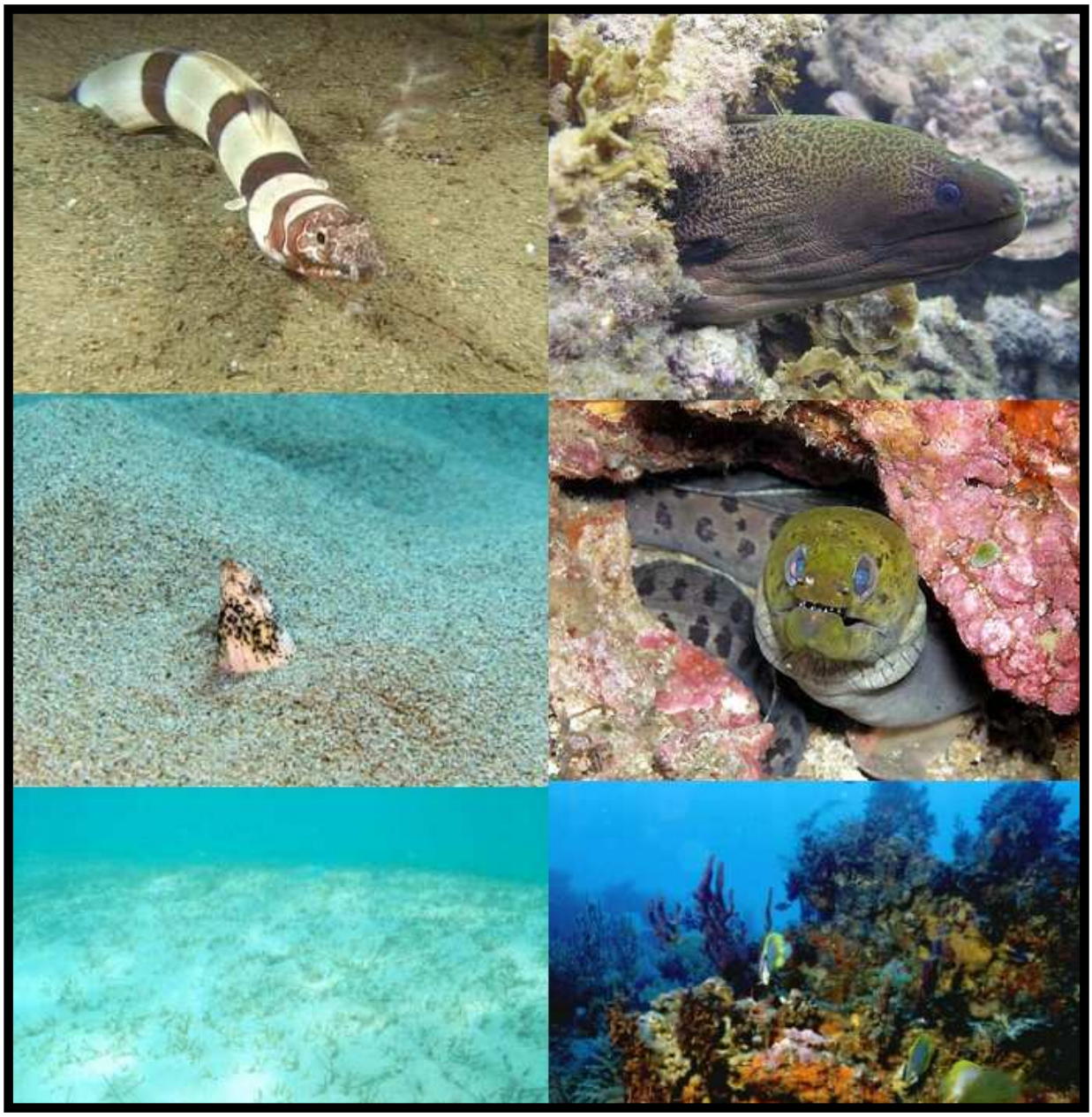

ÉCOLOGIE ALIMENTAIRE

A method to reconstruct anguilliform fishes from partially digested items

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Abstract. Estimating the amounts of resources consumed by individuals is important in many studies. For predators, allometric relationships can be used to extrapolate the size of preys from undigested remains found in the stomach and in the faeces. However, such equations are available for a limited number of species. Based on a large sample size gathered in New Caledonia on both predators (sea kraits) and their preys (anguilliform fishes), we provide the first allometric relationships that allow estimating accurately the mass and the size of various anguilliform fish species.

1 INTRODUCTION

Characterising the diet and estimating the amount of resources consumed by individuals is of central importance in most ecological studies. For many predators, the number and the size of the preys eaten per unit of time are among the key parameters required to address a wide array of biological problems such as those related to the prey-predator relationships, energy budget, intra- or inter-specific competition for instance. Unfortunately, under field conditions, it is often difficult to accurately estimate the dimensions (e.g. body length, body mass) of preys. Indeed, it is almost impossible to measure the food items of predators before they are consumed; afterwards, they are often dilacerated and digested. However, different predators (birds, fishes, reptiles…) swallow their preys as a whole. The use of allometric relationships that links the size and the mass of the prey items can be used to extrapolate their initial dimensions from uneaten fragments, or from undigested remains (e.g. cephalopod beaks, fish otoliths…) found in the stomach and in the faeces (Clarke, 1986; Härkönen, 1986). Although such relationships are species-specific and require a good knowledge of allometric links for the species of interest, this method has been validated and successfully employed in several vertebrate species, notably in seabirds and marine mammals (Duffy & Jackson, 1986; Cherel et al. 2000 and references therein). Extending this approach to poorly studied taxonomic groups would be useful to better understand the diversity of the prey/predators systems.

Typical examples of scantly known assemblages are represented by the fish (preys) and the sea snakes (predators) (Heatwole, 1999). Sea kraits (*Laticauda sp.*) forage in the coral reef ecosystems, and are highly specialized on anguilliform fish (mostly moray, conger and snake eels; Reed et al., 2002; Ineich et al., 2007; Brischoux & Bonnet, 2007). In many areas, these fish are extremely secretive and escape classical sampling methods (underwater visual census or rotenone poisoning, Ackerman & Bellwood, 2000; Willis 2001, Ineich et al., 2007). The snakes swallow their preys as a whole, and it is often possible to obtain their stomach content

through forced regurgitation; thus, they offer a unique opportunity to study anguilliform fish (Reed et al., 2002; Brischoux & Bonnet, 2007; Ineich et al., 2007). However, detailed diet studies are available for three species only, all from the same genus (sea kraits: *Laticauda colubrina,* Heatwole, 1999; *L. saintgironsi* and *L. laticaudata*, Brischoux & Bonnet, 2007; Ineich et al., 2007; *L. semifasciata*, Su et al. 2005). Consequently, there is an almost complete lack of information on these fish communities, several species preyed by the snakes being known from less than 10 specimens (Brischoux & Bonnet, 2007; Ineich et al., 2007). This deficiency of knowledge also means that it is currently impossible to estimate the biomass of the meals of the sea snakes, the fish being partly digested most of the time. Based on a large sample size gathered in New Caledonia, and using a wide range of both intact and partly digested fish, the aim of this study was to provide the first allometric equations that allow estimating the mass and the size of various anguilliform fish species. In the absence of comparable study, one of our first goals was to determine which morphological traits easily available from the stomach remains were the best predictors of the mass (or the size) of the fish.

2 MATERIAL AND METHODS

The study was carried out from 2002 to 2005 on 10 sites located in the southwest lagoon of New Caledonia (9 islets: Ténia, Mba, Signal, Larégnère, Amédée, Porc-Epic, Nouaré, Bayonnaise, Brosse; and a wreck: Ever-Prosperity). Sea kraits are mostly visible when they cross the shore, moving between the sea and the land. The perimeter of each islet was regularly surveyed, both during the day and at night. Most of the snakes were captured by hand and kept in cotton bags until processed. At first capture, the snakes were individually marked by scale clipping (Brischoux and Bonnet, 2007). They were released after completion of the measurements 1h to 24h after capture (Brischoux and Bonnet, 2007). Pooling captures and recaptures, we examined more than 7,000 snakes (> 4,000 individually marked; > 3,000 recaptures). The abdomen of each snake was carefully palpated to detect the presence of a meal.

The prey items were obtained by a gentle massage of the abdomen. Sea-kraits feed mostly on non-spiny fishes and it was easy to force them to regurgitate without risk of injury for the snake. Overall, we obtained 1039 regurgitated prey items belonging to 49 species (37 non-anguilliform fish from 3 species were discarded from the analyses). Stomach contents fell into three broad categories: intact preys (i.e. the skin was undigested), partly digested preys (at least the head and/or the entire tail was intact, depending upon which extremity was swallowed first), and much digested items (e.g. fragments of the tail). One hundred and sixty-eight preys (16% of the total, list of the species in Table 1), probably captured by the snakes shortly before forced regurgitation, were in excellent condition. On these complete fish, we immediately recorded 7 easily accessible morphological traits: body mass (with an electronic scale: ±1g); plus 6 other body-size traits (with a digital calliper: ±0.5cm), (1) total length, (2) snout-vent length (=SVL), (3) tail length from the cloaca to the tip of the tail, (4) body diameter recorded at the level of the head, mid-body, vent, and averaged, (5) eye diameter, and (6) jaw length from the tip of the snout to the most posterior join. Six hundred and twenty five prey items (60%) were partly digested, but at least one of the above measurements was possible. Two hundred and forty six (24%) of the remains were too digested and were considered as useless for our purpose. All the prey items were kept in a 90% alcohol solution, and were later identified to the nearest taxonomy level in the lab.

TABLE 1 - *List of the intact specimens used as references.*

Family	Sub-family	Species	N
Congridae	Congrinae	*Conger* sp.	16
Muraenidae	Muraeninae	*Cirrimaxilla formosa*	3
Muraenidae	Muraeninae	*Echidna unicolor*	1
Muraenidae	Muraeninae	*Enchelycore pardalis*	5
Muraenidae	Muraeninae	*Gymnothorax albimarginatus*	1
Muraenidae	Muraeninae	*Gymnothorax chilospilus*	67
Muraenidae	Muraeninae	*Gymnothorax eurostus*	10
Muraenidae	Muraeninae	*Gymnothorax fimbriatus*	8
Muraenidae	Muraeninae	*Gymnothorax formosus*	1
Muraenidae	Muraeninae	*Gymnothorax fuscomaculatus*	2
Muraenidae	Muraeninae	*Gymnothorax margaritoforus*	7
Muraenidae	Muraeninae	*Gymnothorax moluccensis*	5
Muraenidae	Muraeninae	*Gymnothorax pindae*	7
Muraenidae	Muraeninae	*Gymnothorax reticularis*	1
Muraenidae	Muraeninae	*Gymnothorax richardsonii*	2
Muraenidae	Muraeninae	*Gymnothorax* sp.	1
Muraenidae	Muraeninae	*Gymnothorax undulatus*	5
Muraenidae	Muraeninae	*Gymnothorax zonipectis*	2
Muraenidae	Uropterygiinae	*Anarchias allardicei*	2
Muraenidae	Uropterygiinae	*Anarchias cantonensis*	2
Muraenidae	Uropterygiinae	*Anarchias seychellensis*	1
Muraenidae	Uropterygiinae	*Anarchias* sp.	1
Muraenidae	Uropterygiinae	*Scuticaria tigrina*	3
Muraenidae	Uropterygiinae	*Uropterygius alboguttatus*	1
Muraenidae	Uropterygiinae	*Uropterygius concolor*	1
Muraenidae	Uropterygiinae	*Uropterygius macrocephalus*	1
Muraenidae	Uropterygiinae	*Uropterygius* sp.	1
Muraenidae	unidentified	unidentified	4
Ophichthidae	Myrophinae	*Muraenichthys* sp.	5
Ophichthidae	Myrophinae	*Myrophis microchir*	1
Ophichthidae	Ophichthinae	*Myrichtys maculosus*	1

3 Results

3.1 Estimating the length of the prey

In order to identify the best predictor of total length, we performed stepwise multiple regressions (forward *versus* backward regressions led to similar results) with the total length of the prey as the dependent variable, and the six other traits as the independent variables. We first run the analyses by including all fish species. Then, we made a distinction between the two main taxonomic groups (the Ophichthidae sample size was too small to perform the tests separately). Table 2 summarises the results.

TABLE 2 - *Stepwise multiple regressions between total length or body mass as dependent variables and all other morphological traits as the predictive variables (see text). By including the other variables (e.g. diameter…), the proportion of explained variance never increased by more than 2%, we thus displayed in this table only the first significant predictor. All the variables were Ln-transformed to meet linearity. SVL: snout-vent length, Tail L: tail length, Ø $_{mid}$: diameter of the body recorded at mid-body, Ø $_{vent}$: diameter of the body recorded at the vent, Ø $_{mean}$: averaged body diameters.*

Family	Sub-family	Dependant Variable	Predictive Variable	R^2	F	beta	P
All		Length	SVL	0.94	1475.81	0.97	<0.0001
		Mass	Ø $_{mean}$	0.91	981.87	0.96	<0.0001
Congridae		Length	Tail L	0.99	1014.26	0.99	<0.0001
		Mass	Ø $_{mid}$	0.99	3081.83	0.99	<0.0001
Muraenidae	All	Length	SVL	0.96	2548.79	0.98	<0.0001
		Mass	Ø $_{mean}$	0.92	1070.43	0.96	<0.0001
	Muraeninae	Length	SVL	0.96	1856.19	0.98	<0.0001
		Mass	Ø $_{mean}$	0.94	1179.30	0.97	<0.0001
	Uropterigiinae	Length	SVL	0.97	2548.79	0.98	<0.0001
		Mass	Ø $_{vent}$	0.98	389.31	0.99	<0.0001

Snout vent length was the best predictor in most cases, whilst tail length was the first trait retained for the Congridae. Overall, using snout vent length and/or tail length it was possible to estimate accurately the total size of the fish (all the models had $0.94<R^2<0.99$). However, one of these traits was available for only 34% of the partly digested fish. Therefore, we examined if the other morphological traits sampled on more digested items (i.e. when > half of the fish was digested) could be employed confidently. Simple regressions (either all the fish pooled or grouped by family) suggested that even well digested prey items could be used to estimate the total length of the fish as the error remained acceptable using body diameter ($0.70<r^2<0.96$), and jaw length ($0.69<r^2<0.86$). The diameter of the eye, poorly correlated to the length of the fish, was useless ($0.49<r^2<0.52$) (all $P<0.001$).

3.2 Estimating the mass of the prey

As above, we used stepwise/simple regressions procedure with the mass of the prey as the dependent variable. The body diameter of the prey was the best predictor in most cases (Table 2). Fortunately, in the partly digested preys, this parameter was available in most cases (68%). We also examined if the other traits could be used when the body diameter was unavailable. SVL ($0.83<r^2<0.97$), tail length ($0.72<r^2<0.97$), total body length ($0.91<r^2<0.98$), jaw length ($0.89<r^2<0.95$) and the eye diameter ($0.52<r^2<0.87$) were all useful characters to estimate the mass of the fish (all $P<0.001$).

The accuracy to estimate the mass of the prey is a key parameter, notably in terms of energy budget. Therefore, we further tested the validity of our method. First, we randomly divided our sample of intact preys in two sub-samples of 84 intact fish each. We used the first set to calculate the equation that links body diameter (independent variable) and body mass (dependant variable). The terms of the regression were Ln body mass=2.5353*Ln mean diameter–3.3953 ($F=1020.62$, $df=1, 84$, $r^2=0.93$, $p<0.0001$). Then, we applied the equation to the second data set in order to compare the estimated mass with the actual mass of these fish: there was no

significant difference between the predicted and the measured body mass (paired t-test, t=-1.33, df=83, p=0.18). Finally, we re-calculated the terms of the equation using the whole data set of intact preys (N=168), and calculated the mean error when predicting the mass of the fish (=difference between predicted and observed values expressed as 100 (measured body mass – predicted body mass)/maximum (measured body mass; predicted body mass)). On average, our error was small: 7.73±8.89%. A more focused analysis restricted to the Muraeninae, revealed an equivalent average error (6.58±7.76%).

4 Conclusion

The anguilliform fish/sea kraits system is somewhat unique for several reasons. The large spectrum of poorly known fish (>30 species) and the availability of undigested preys provided an ideal reference set to reconstruct partly digested items. Therefore, it was possible to use the sea kraits as powerful sampling tools to gather the main morphological characteristics of yet neglected fish communities (Ineich et al. in press). Many of the anguilliform fish found in the stomach of the snakes contained eggs or secondary preys (e.g. remains of crustaceans). Reconstructing the size of the preys is crucial to assess questions related to their reproduction (e.g. size at maturity), and diet. Similarly, the length-size relationships we provide (Appendix) could be valuable for studies that deal with the biomass of reef fish. Notably, there is yet little information for tropical anguilliform fish (Kulbicki et al. 2005). On the other hand, thanks to the allometric equations derived from the intact preys, the dimensions of the snake preys could be accurately estimated in 76% of the cases. Sea kraits, as most snake species, are gape-limited predators and swallow their prey whole (Greene 1983). Obtaining accurate data on both the size and the mass of their prey is essential to address a wide array of biological problems such as those related to the prey-predator relationships, energy budget, intra- or inter-specific competition for instance.

Overall our simple method enables to fill up a gap of knowledge that concerns both the anguilliform fish and sea snake ecology. The method and equations presented at the end of this paper (Appendix) offer two advantages: they are accurate and simple to use.

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APPENDIX 1 - *Length-mass, mass-mean diameter and length-mean diameter relationships for new caledonian anguilliform fishes. For each taxonomic level, the equation, the regression parameters (F, r² and P-value) and the number of specimens used (N) are given. BM, TL and MD stand for body mass, total length and mean diameter respectively.*

Family	Sub-family	Species	Equation	F	r²	P-value	N
All			Ln(BM) =2.87*Ln(TL)-6.36	1173.67	0.88	<0.0001	168
			Ln(BM) =2.60*Ln(MD)-3.56	1893.37	0.92	<0.0001	161
			Ln(TL) = 0.73*Ln(MD)+1.40	384.05	0.70	<0.0001	163
Congridae	Congrinae	*Conger sp.*	Ln(BM) =3.37*Ln(TL)-8.21	841.82	0.99	<0.0001	12
			Ln(BM) =2.99*Ln(MD)-4.55	582.97	0.98	<0.0001	14
			Ln(TL) =0.86*Ln(MD)+1.17	223.23	0.95	<0.0001	13
Muraenidae	All		Ln(BM) =2.90*Ln(TL)-6.40	1312.40	0.90	<0.0001	140
			Ln(BM)=2.60*Ln(MD)-3.60	1821.32	0.93	<0.0001	142
			Ln(TL)=0.78*Ln(MD)+1.26	490.35	0.78	<0.0001	143
	Muraeninae		Ln(BM)=3.05*Ln(TL)-6.87	1255.89	0.91	<0.0001	128
			Ln(BM)=2.53*Ln(MD)-3.45	2197.76	0.94	<0.0001	130
			Ln(TL)=0.74*Ln(MD)+1.32	700.46	0.84	<0.0001	130
		G. chilospilus	Ln(BM)=3.31*Ln(TL)-7.71	1007.88	0.94	<0.0001	63
			Ln(BM)=2.46*Ln(MD)-3.25	893.31	0.93	<0.0001	65
			Ln(TL)=0.71*Ln(MD)+1.43	645.64	0.91	<0.0001	65
		G. eurostus	Ln(BM)=3.42*Ln(TL)-7.87	440.94	0.98	<0.0001	10
			Ln(BM)=2.29*Ln(MD)-2.74	193.75	0.96	<0.0001	10
			Ln(TL)=0.56*Ln(MD)+1.53	139.02	0.94	<0.0001	10
		G. fimbriatus	Ln(BM)=3.32*Ln(TL)-7.86	308.79	0.98	<0.0001	8
			Ln(BM)=2.55*Ln(MD)-3.52	393.65	0.98	<0.0001	8
			Ln(TL)=0.75*Ln(MD)+1.34	230.27	0.97	<0.0001	8
		G. margaritophorus	Ln(BM)=1.61*Ln(TL)-1.86	19.42	0.79	<0.007	7
			Ln(BM)=2.56*Ln(MD)-3.52	87.79	0.94	<0.0003	7
			Ln(TL)=1.31*Ln(MD)-0.27	20.73	0.80	<0.007	7
	Uropterigiinae		Ln(BM)=2.61*Ln(TL)-5.86	342.54	0.97	<0.0001	12
			Ln(BM)=3.21*Ln(MD)-4.67	200.39	0.95	<0.0001	12
			Ln(TL)=1.16*Ln(MD)+0.61	76.86	0.87	<0.0001	13

Foraging ecology of sea kraits (Laticauda spp.) in the Neo-Caledonian Lagoon

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Abstract. To understand the magnitude and ecological impact of predation, we need to know not only predator abundance and feeding rates, but also the area from which the prey are taken. Previous work on amphibious sea-snakes (sea kraits) in New Caledonia has documented the former parameters, and suggested that these marine snakes may be major predators of anguilliform fish within coral-reef ecosystems. To estimate the area over which these snakes forage, we developed a method based on detailed assessments of (1) the eel species consumed (and hence, their habitats of origin), (2) the state of digestion (and hence, time since capture) of prey items inside snakes returning to their home islands after foraging trips; and (3) the rate of digestion of prey in experimental trials. In combination with data on rates of snake movement, we conclude that one species (*Laticauda laticaudata*) forages mostly on soft-bottom habitats within 23 km of the home island, whereas the other species (*L. saintgironsi*) forages on coral substrates within 38 km of the home island. The distribution of estimated foraging ranges was similar between these two species (about one-third of prey taken within a few kilometres of the home island; the rest from a wide range of much further sites), despite interspecific divergence in traits such as prey types, prey sizes, and rates of digestion. These extensive foraging ranges suggest that sea kraits are predators of eels over the entire area of the lagoon; and imply that populations of these top predators can be affected by disturbance to prey resources even many kilometres from the home island.

KEY WORDS: sea snakes, diet, foraging range, foraging habitat

1 INTRODUCTION

In many marine ecosystems, some of the most significant predators are air-breathing animals such as birds and seals, that forage in the ocean but return to land for other activities such as resting and breeding (central place foragers; Elliott 1988). Typically, such animals have a consistent terrestrial home (usually, on an island) to which they return after foraging trips. Studies on the feeding habits of such predators can clarify not only their trophic biology, but also the distribution and ecology of prey species that otherwise are difficult to monitor (Cherel et al. 2004). Hence, these predators can serve as valuable bioindicators in marine ecosystems (Guinet et al. 2001, Hindell et al. 2003). Measuring the quantities and species composition of prey consumption is relatively straightforward, by observing predators returning to their terrestrial home after foraging trips. However, one critical variable remains difficult to assess: the geographic extent of foraging. Clearly, the intensity of predation may be greater if it is concentrated in a small area around the home island, than if predators disperse long distances in their search for prey. Biologists studying seabirds and pinnipeds have utilized small tracking devices to answer this question, but these devices are too large to attach to smaller types of predators. In the present paper we explore the geographic extent of foraging by another type of land-based marine predator that so far has attracted far less scientific attention: sea-snakes of the genus *Laticauda*.

Unlike the other major lineage of marine snakes (the hydrophiines), laticaudines ("sea kraits") are oviparous animals that forage in the ocean but return to land to mate, lay their eggs, digest their prey, and slough their skins (Heatwole 1999). Although laticaudines are abundant through many islands of the Indo-Pacific (Heatwole 1999), their ecological role in coral-reef systems remains unclear. Our detailed mark-recapture studies on two laticaudine species on a small island in the Neo-Caledonian Lagoon of New Caledonia have revealed very high population densities (> 1,500 snakes on a 6-ha islet), a high degree of philopatry (snakes are rarely re-captured on any island other than the one on which they were first seen),

and a total consumption of prey biomass comprising > 950 kg of anguilliform fish (henceforth "eels" for simplicity) per annum. The eels on which these snakes prey are difficult to survey by any available technique, and thus the overall abundance of eels in these systems remains unknown (Ineich et al. 2007). The consumption rates suggest that snakes are top predators in this system, but we cannot fully interpret these data without knowing the size of the area over which the snakes collect their prey.

Because direct monitoring of snake movements during foraging bouts is difficult, we are forced to rely on indirect means. The current paper outlines our solution to this problem, based upon measures of:

(1) the types of eels consumed by each of our two laticaudine study species; because such eels are habitat-specific, we can then assess the habitat types from which the snakes obtain their prey;

(2) the degree of digestion of prey items inside snakes captured at the end of foraging bouts, as they return to their home island (Fig. 1); and

(3) the rate at which snakes digest their prey (based upon experimental trials) which, in combination with states of digestion (see [2] above) allows us to estimate the time interval between a snake capturing an eel and returning to land.

These data can then be combined with existing information on the distribution of habitat types within the Neo-Caledonian Lagoon, and on swimming speeds of sea kraits, to estimate the geographic extent of the area over which sea kraits forage for their prey.

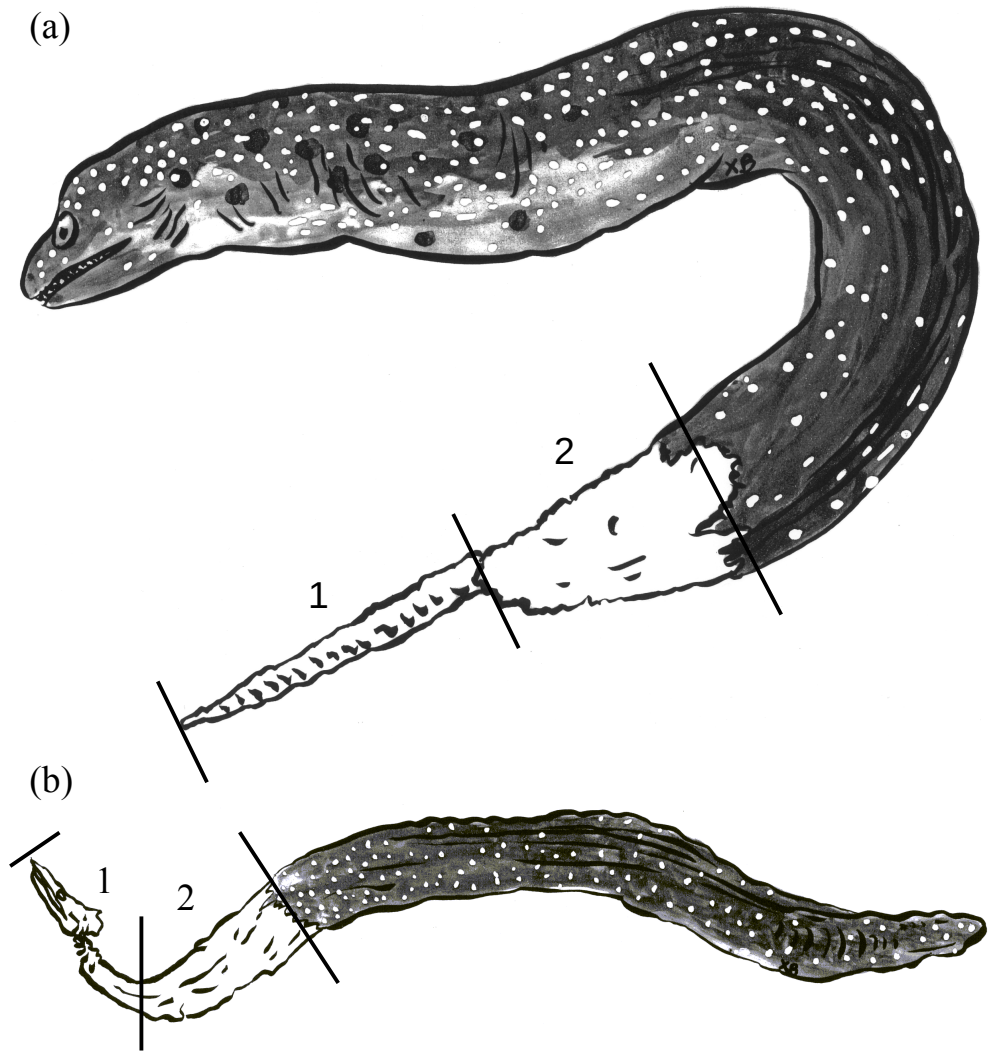

FIG. 1 - *Specimens of regurgitated moray eels (*Gymnothorax eurostus*). Note that the extremity first swallowed, (a) tail or (b) head, is progressively digested while the rest of the prey remains intact. 1: already digested part (only some vertebrae or the skull remain) and 2: segment of the prey under digestion when the regurgitation occurred. Drawings (XB) after pictures of freshly regurgitated items, specimens #121 and #167 deposited in the sea krait prey collection of the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS UPR 1934).*

2 MATERIAL AND METHODS

2.1 Study species and general methods

Two species of sea kraits (Elapidae, Hydrophiinae) occur in New Caledonia: the endemic *Laticauda saintgironsi* (Cogger & Heatwole 2006) and the widespread *L. laticaudata* (Ineich & Laboute 2002, Saint Girons 1964). Both are elongate brightly-banded species attaining approximately 1.5 m in maximum length. We surveyed sea krait populations on 9 different islets in the southwest lagoon of New Caledonia (Brischoux & Bonnet 2007).

Snakes were collected by hand from the islands, measured (snout vent length-SVL, ±1cm), weighed (±1g) and individually marked by scale clipping (Brischoux & Bonnet 2007). The abdomen of each snake was palpated to check for the presence of prey in the stomach. Because the eels consumed by sea kraits are slender and non-spinose, the snakes readily regurgitate their prey if gentle pressure is applied to the rear of the stomach (Brischoux & Bonnet 2007). We collected, identified, measured and preserved 1,077 regurgitated prey items (Böhlke et al. 1999, Smith 1999a, b, Smith & McCosker, 1999, see Brischoux et al. 2007). We quantified niche overlap between the two sea krait species with the Morisita-Horn similarity index (Magurran 1988, 2004), using EstimateS 7.5. software (Colwell 2005). To infer the habitats from which eels had been captured, we used FishBase (Froese & Pauly 2006) to extract information on 29 of the 49 eel species eaten by the sea-kraits (habitats of the other taxa are not yet known). For simplicity, we categorised habitats into three broad types: hard bottom, soft bottom and hard plus soft bottom. For example, habitats such as "rubble, coralline crevices, coral heads…" were considered as hard bottom, whereeas "sandy gravel bottom, sand slope, estuaries …" were considered as soft bottom.

2.2 Elapsed time between prey capture and the snake's return to land

We palpated 309 prey items from snakes that were collected as they returned to the home island (<1h after arrival), resulting in prey items that ranged from well-digested to almost intact. For each prey item, we measured the diameter and the length of the undigested fish or fragment, calculated the state of digestion, and estimated the total initial length of the prey using allometric equations linking body measurements to total length (see Brischoux et al. 2007 for details; Fig. 1).

To quantify rates of digestion, we captured 18 *Laticauda laticaudata* and 19 *L. saintgironsi* as they came ashore with a prey item in the stomach, and kept them in captivity in an outdoor arena (1.2 X 1.2 m) until digestion was complete. Because the rate of digestion by snakes is sensitive to temperature (Naulleau 1983), we measured snake temperatures in the experimental arena once every two hours with an infrared laser thermometer (Raytek MX2). Body temperatures of free-ranging foraging snakes were recorded using surgically-implanted temperature loggers (LTD-1110, Lotek Wireless Inc., Canada). Thermal regimes for snakes digesting prey in the experimental arena (mean±SD, 27.6±1.6°C) were very similar to those of aquatic foragers (26.5±0.8°C).

Because the fishes are very large relative to the snakes that eat them, and the snake's body wall is very thin compared to the diameter of the fish, it is possible to measure the length and diameter of prey items in a snake's stomach *in situ* by careful palpation (see Shine & Sun 2003 for validation of this method). We measured the length and diameter of the prey every 12h until completion of digestion, as indicated by the absence of objects in the abdomen. Using allometric equations linking the length and the diameter of the prey, we estimated initial prey length (Brischoux et al. 2007; mean error < 8%), and thus could calculate the rate of digestion. Knowing the state of digestion of prey in snakes returning to their home island after foraging trips (above), we could estimate the duration of time that had elapsed between the capture of prey and the snake's arrival on land.

3 Results

3.1 Composition of diet

We recorded a diverse array of fishes from the alimentary tracts of sea kraits, comprising 49 species in total. Of these, only 13 were shared by the two sea-krait species, indicating a clear interspecific dietary divergence (Table 1). Moreover, the shared species were infrequently recorded in at least one of the sea krait species (Table 1). These effects translated into a low value of the Morisita-Horn similarity index: 0.15 (Magurran 1988, 2004). *Laticauda saintgironsi* fed on a wider prey spectrum than did *L. laticaudata* (38 versus 24 prey-species respectively, Table 1). However, one abundant species (*Gymnothorax chilospilus*) constituted most of the *L. saintgironsi* diet (46% of prey items: see Table 1). In contrast, more than half of the *L. laticaudata* diet was comprised of three eel species (*Gymnothorax albimarginatus*, *Muraenichtys* sp., *Conger cinereus*; Table 1).

TABLE 1 - *List of the fish species identified from sea kraits stomach contents, with their percentage in each diet (*L. laticaudata *and* L. saintgironsi*, LL and LS respectively). Sample sizes were N=365 prey items for* L. laticaudata *and N=655 for* L. saintgironsi*. Habitats were extracted from FishBase (Froese & Pauly 2006). Species in bold comprise more than 10% of the sea krait diets.*

Prey species	% of diet of LL	% of diet of LS	Habitat
Anarchias allardicei	0.5	0.4	
A. cantonensis	0	1.8	
A. seychellensis	0	0.4	hard
A. sp.	0	0.3	
Cirrimaxilla formosa	2.7	0.7	
Conger cinereus	23.2	3.2	hard/soft
Echidna sp.	0	0.3	
E. unicolor	0	0.4	
Enchelycore pardalis	0	1.5	hard

Prey species	% of diet of LL	% of diet of LS	Habitat
Gymnothorax albimarginatus	20.5	0	soft
G. chilospilus	4.3	46.2	hard
G. cribroris	0.3	0	hard
G. dorsalis	0.3	0.3	
G. eurostus	0.5	6.4	hard
G. fimbriatus	0	4.8	hard
G. formosus	0	1.6	
G. fuscomaculatus	0	0.9	hard
G. margaritoforus	0	5.6	hard
G. moluccensis	8.1	0.3	
G. nudivomer	0.5	0	hard
G. pindae	0.3	5.7	hard
G. pseudothyrsoideus	0	1.1	
G. reevesi	0.3	1.0	
G. reticularis	3.2	0	soft
G. richardsonii	1.3	1.2	hard
G. sp.1	0	0.3	
G. sp.2	1.3	0	
G. undulatus	0	1.2	hard
G. zonipectis	0	1.3	hard
Muraenichthys sp.	10.5	0	soft
Myrichtys maculosus	1.1	0	soft
Myrophis microchir	8.1	0	
Plotosus lineatus	2.7	0	hard/soft
Ptereleotris sp.	8.1	0	hard/soft
Scuticaria okinawae	0	0.4	
S. sp.	0	0.4	
S. tigrina	0	2.3	hard/soft
Strophidon sathete	0.3	0.1	soft
Uropterygius alboguttatus	0	0.6	hard
U. concolor	1.1	1.8	hard/soft
U. fuscoguttatus	0	0.6	hard
U. macrocephalus	0	0.4	hard
U. polyspilus	0	1.0	hard
U. sp. 14b	0.3	1.0	
U. supraforatus	0	2.0	hard
U. xanthopterus	0	0.3	hard
Unidentified fish	0.5	0	
Unidentified Muraeninae 1	0	1.1	
Unidentified Muraeninae 2	0	1.1	

3.2 Prey habitat

Combining these data on prey species with habitat-use information from FishBase (Froese & Pauly 2006), the two sea krait species foraged in different places (Yates χ^2=591.77, df=2, p<0.0001, Fig. 2). *Laticauda saintgironsi* fed on prey from hard substrates (mainly within the coral matrix) whereas *L. laticaudata* fed extensively on eel species from soft-bottom habitats.

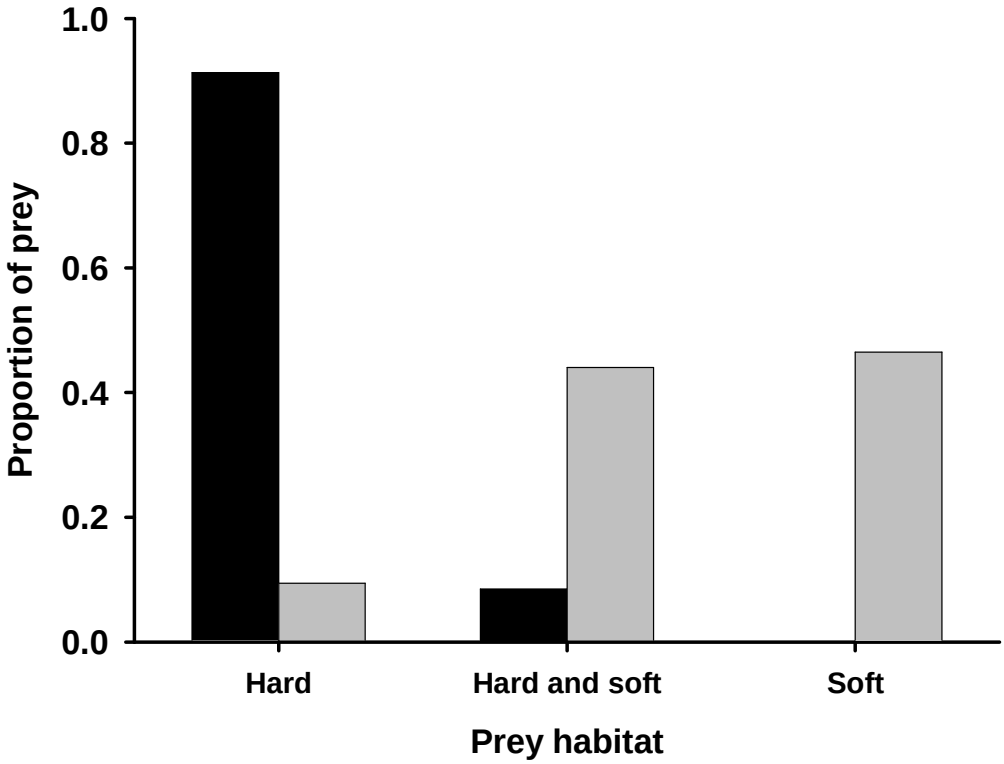

FIG. 2 - *Proportion of sea krait prey taken from three types of habitat. Black bars and grey bars show data for* L. saintgironsi *and* L. laticaudata *respectively. Due to unknown habitats of several prey species (see material and methods) and to unidentified prey items, sample size were N=590 and N=286 for* L. laticaudata *and* L. saintgironsi *respectively.*

3.3 Rate of digestion of the prey

All of the anguilliform prey items that we examined were partially digested from either the anterior or posterior end of the body, but remained intact at the other extremity (Fig. 1). Hence, the rate of digestion can be quantified on a linear axis, corresponding to the proportion of eel length remaining undigested. The 37 snakes kept captive until completion of digestion provided overall mean values for digestive duration similar to previous records (8 days in *L. colubrina*: Shetty & Shine 2002b; 6 days in *Laticauda saintgironsi* and *L. laticaudata*: Ineich et al. 2007). However, we have more detail than in these previous studies: for example, our data show that the proportion of the prey item that is digested increases almost linearly with time, as expected from the symmetric cylindrical morphology of these items.

Relative to body size, *Laticauda saintgironsi* ate longer prey items than did *L. laticaudata* (means 34.39±0.43 versus 31.95±0.44 cm respectively; ANCOVA with SVL as covariate, $F=14.60$, $df=1$, $p<0.0001$). As expected, initial prey size (length) relative to snake size affected the rate of digestion (Spearman correlation, $p<0.05$). Accordingly, digestion speeds differed between the two snake species (ANOVA, $F=5.06$, $df=1$, $p=0.03$; 20.6±0.08% of the prey being digested per day *versus* 16.2±0.04% respectively).

3.4 Elapsed time between prey capture and arrival on land

Both species displayed markedly bimodal distributions of the estimated duration of time between prey capture and return to the home island (Fig. 3). Approximately one third of prey items (26.7% and 33.6% for *Laticauda laticaudata* and *L. saintgironsi* respectively, Yates $\chi^2=0.25$, $p=0.71$ comparing the 2 species) were essentially undigested, with only a small portion of skin affected and no impact on prey length. Because sea kraits are relatively slow swimmers (Shine et al. 2003b), these undigested items presumably were captured close to land (≤0.5 days, henceforth "short foraging trips"). The remaining two-thirds of prey items were partially digested, sometimes to the point that only the head or the tail of the eel remained in

the snake's stomach. These prey items were captured more than 0.5 days before arrival on land, and often over much longer periods (Fig. 2; henceforth, "long foraging trips"). Looking only at these long trips, *L. laticaudata* tended to return land more rapidly after feeding than did *L. saintgironsi* (ANOVA, $F=19.0$, $df=1$, $p<0.0001$; 1.65±0.09, max: 3.05 days for *L. laticaudata* versus 2.29±0.08, max: 4.74 days for *L. saintgironsi*; Fig. 3). Initial prey length was negatively correlated with return trip duration in *L. saintgironsi* (i.e., snakes taking larger prey returned to land more rapidly; $F=12.64$, $df=1.15$, $p<0.001$), but this effect was weak, explaining only 7% of the variance in elapsed times.

4 Discussion

The method that we have developed to estimate the duration of foraging trips in sea kraits relies on a crucial assumption: that as soon as it captures a prey item, a sea krait returns to land. This assumption is supported by previous reports of snake behaviour (e.g., Saint Girons 1964; Guinea 1986) and by the marked impairment of a snake's swimming ability caused by a prey item in the stomach (Shine & Shetty 2001b). Sea kraits are vulnerable to predators such as sharks (Ineich & Laboute 2002) and thus, apparently return to land as soon as they have fed. In keeping with this argument, 86% of the snakes that we captured coming ashore had a prey in the stomach. Thus, the state of digestion of a prey item inside a snake returning to shore should provide a reliable indication not only of the time that has elapsed since that prey item was consumed, but also of the duration of the snake's return trip from its foraging grounds to its home island.

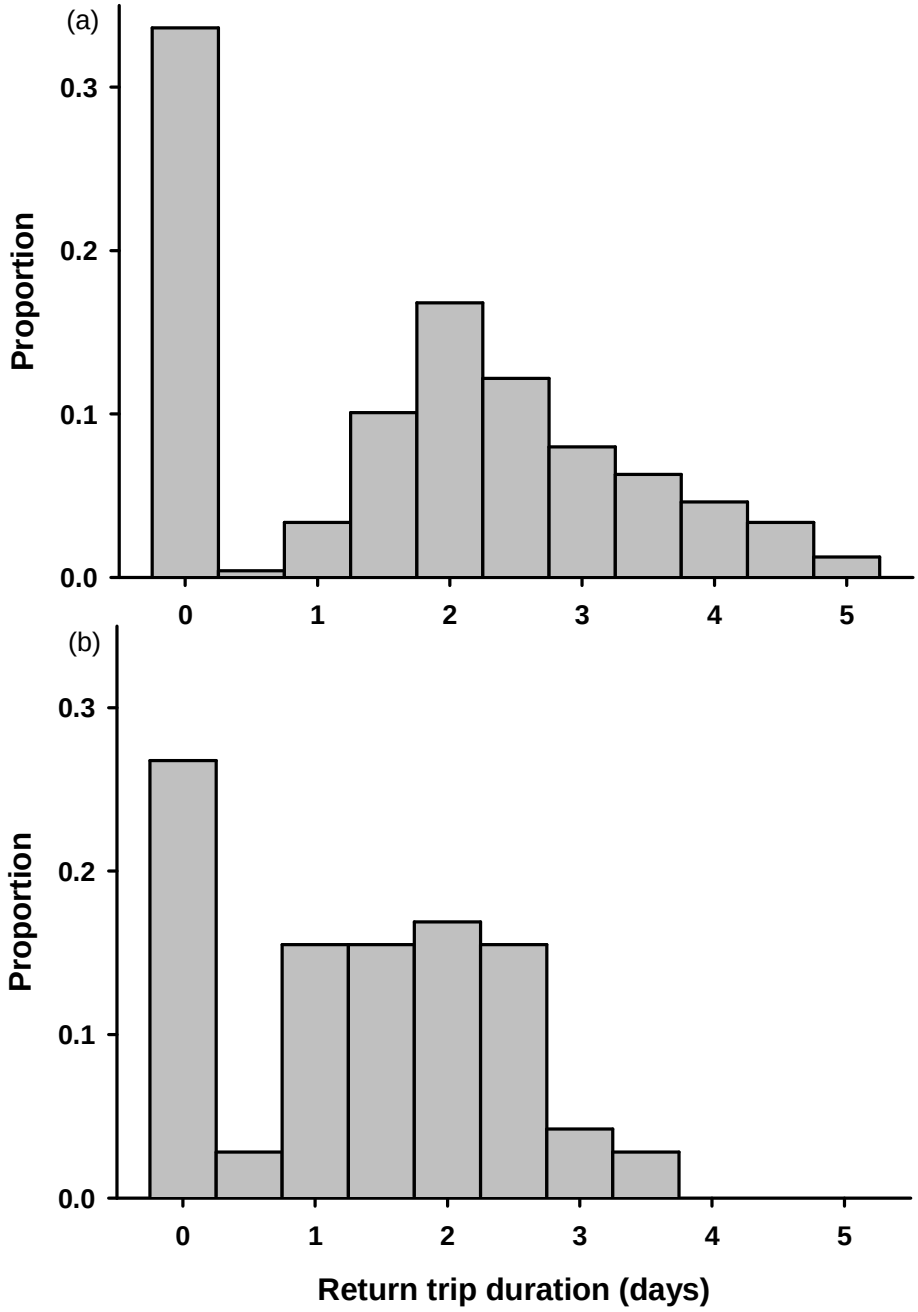

FIG. 3 - *Distribution of estimated return trip duration for the sea kraits* Laticauda saintgironsi *(a) and* L. laticaudata *(b). Estimated trip durations were calculated from 220 prey fragments for* L. saintgironsi *and 68 for* L. laticaudata.

The bimodal distribution of return-trip durations suggests that these snakes obtain about one-third of their prey from short foraging trips close to their own home island, but that the rest of their food intake comes from a much wider area. The lack of intermediate durations (return trips 0.5 to 1 day long) suggests a clear geographic demarcation between these two sites. The similarity in trip durations between the two sea krait species is surprising, given the divergence in prey types between these taxa. Data on prey ecology suggest that *Laticauda saintgironsi* feeds mostly on eel species that live in crevices of hard bottom habitats (coral, rubble, rock) whereas *L. laticaudata* tends to feed on species living in burrows on soft bottom habitats (seagrass beds, mud flats, sand). Reef flats close to the home island provide both environments (Andréfouët 2002), but if snakes move beyond these areas they presumably move longer distances to specific habitat types (isolated coral patches, reef flats or the barrier reef for *L. saintgironsi*; vast soft-bottom areas of the lagoon for *L. laticaudata*).

Can we specify the geographic location of these foraging sites more precisely, by translating the duration of return trip into distances travelled by recently-fed snakes? Both sea krait species exhibit similar speeds while swimming (c.a. 0.3 $m.s^{-1}$, unpublished data from Time-Depth Recorders) but typical movements (even after feeding) consist of multiple dives that decrease their linear swimming speed (to about 0.1 $m.s^{-1}$; unpublished data from Time-Depth Recorders). Focusing on Signal islet, a typical islet of the lagoon, we calculate that sea kraits capture one third of their prey very close to the islet, presumably on the reef flat (45% hard bottom, 55% soft bottom; Andréfouët 2002). The remaining prey items are taken from much further away, in a mean radius of 14 km (max: 23 km) for *Laticauda laticaudata* and of 21 km (max: 38 km) for *L. saintgironsi* (Fig. 4). Interestingly, the minimum estimated distance for "long foraging trips" is 3 km for *L. saintgironsi*, corresponding to the closest reef flats situated south of Signal islet (Fig. 4). For *L. laticaudata*, this minimum distance is smaller (1 km) and accords well with the widespread availability of soft bottom areas in the lagoon.

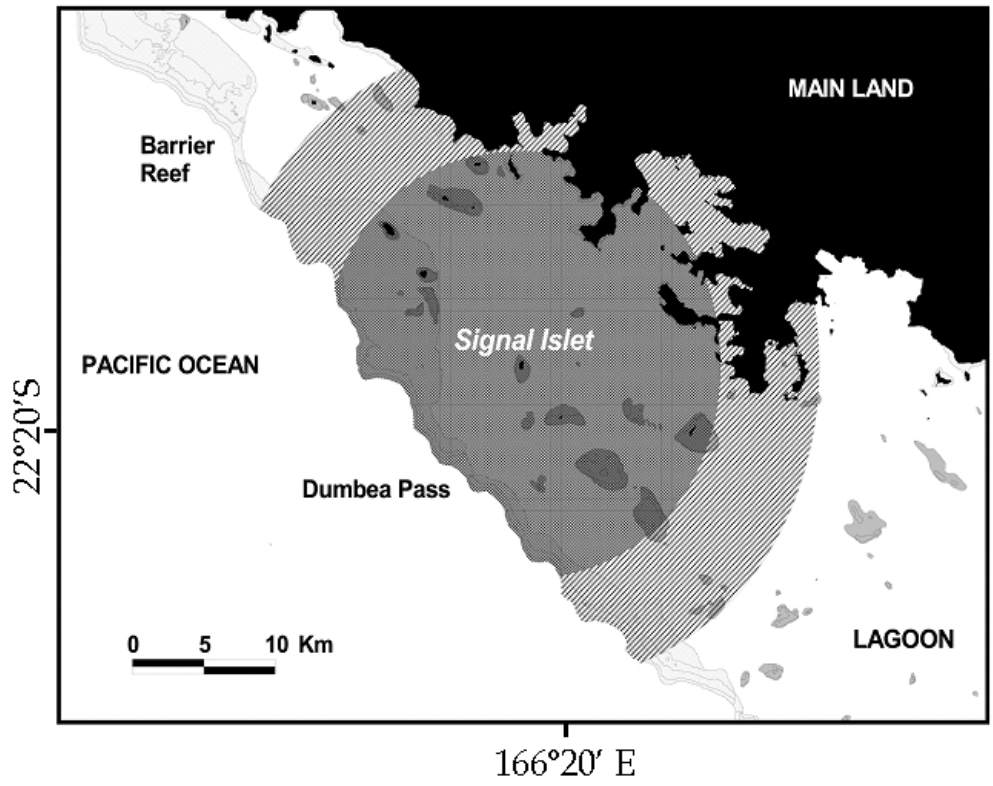

FIG. 4 - *Estimated mean foraging ranges of the sea krait population of Signal islet (dark circle for* L. laticaudata *[mean radius of 14km], light grey circle for* L. saintgironsi *[mean radius of 21 km]). Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by light grey areas.*

These results significantly expand our view of the spatial scale over which sea kraits forage in the lagoon ecosystem (see Ineich et al. 2007). A single snake population can exploit a massive ocean area (at least 615 km² surface area for *L. laticaudata* and 1, 380 km² for *L. saintgironsi*; perhaps up to 1, 660 km² for *L. laticaudata* and 4,500 km² for *L. saintgironsi*). This result reinforces the position of sea kraits as top predators of the lagoon (Ineich et al. 2007): given that most islets in New Caledonia host snake populations, virtually the entire sea floor of the lagoon

can be prospected by sea kraits (Fig. 4, see http://www.shom.fr/ for maps). Accordingly, in term of conservation, disturbances (pollution, over-fishing and coral reef destruction, Walker & Ormond 1982; Linden 1999; Hughes et al. 2003; Riegl 2003) that influence local eel communities can reverberate over huge distances to influence predators based at islands many kilometres distant. Hence, the spatial scales of currently protected areas (usually a few hundred km²) need to be reconsidered. Conversely, disturbance to a home island (e.g., extermination of snakes due to resort construction, pers. obs.) might greatly affect predation pressure on anguilliform fishes over a massive spatial scale.

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Determinants of dietary specialization: a comparison of two sympatric species of sea snakes

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Abstract. Why do some predator species specialize on only a single type of prey whereas others take a broad range? One critical determinant may be the ontogenetic range of body sizes of the predator compared to that of its prey: if any single prey taxon spans only part of the range of prey sizes ingestible by the predator, then the predator will be more likely to take multiple prey taxa. We exploit a model system that provides a robust opportunity to test this hypothesis: two sympatric species of predatory sea snakes, similar in size and general ecology, that feed on anguilliform fishes from different habitats in the Great Lagoon of New Caledonia. Eel species from soft-bottom habitats must construct their own burrows, and thus tend to be more slender-bodied and less variable in body size than are eel species that inhabit variable-sized crevices among hard coral. As a result, a laticaudine sea snake species (*Laticauda saintgironsi*) that feeds on hard-coral-dwelling eels relies primarily on a single prey species; juvenile snakes take young eels whereas adult snakes consume adult eels of the same species. In contrast, a laticaudine species (*L. laticaudata*) that forages for soft-bottom eels switches its prey ontogenetically: juvenile snakes take small eel species whereas adult snakes consume large eel species. Thus, habitat-imposed constraints on the range of body sizes within each prey taxon ultimately generate a striking difference in the degree of dietary specialization of two closely related, sympatric predator species.

KEY WORDS: Elapidae, feeding habits, prey diversity, sea krait, trophic niche

1 INTRODUCTION

The trophic relationships of living organisms encompass a remarkable diversity, and understanding the factors that shape each species' niche remains a major challenge for ecological theory (Tokeshi 1999). One of the most fundamental questions concerns dietary breadth: why are some organisms specialized to feed on only one or a few types of prey, whereas closely related organisms take a diverse array of prey taxa? Dietary diversity has strong ramifications for issues such as trophic web complexity (and hence, perhaps, stability: Finke and Denno 2004), and the degree to which fluctuations in a single prey taxon can influence resource availability for a predator species (Stenseth et al. 1998, Salamolard et al. 2000, Madsen et al. 2006). Because different prey species often occur in different places or are vulnerable at different times, or can be hunted most effectively in different ways, dietary diversity can feed back into many other facets of a predator species' ecology (Peckarsky 1982).

Most major lineages of predators include both specialized and generalized taxa in terms of diet breadth (McDonald 2002; Steenhof and Kochert 1988; Glodek and Voris 1982; Nyffeler 1999; Holbrook and Schmitt 1992). There are multiple causal influences on dietary diversity (Peckarsky 1982; Greene 1986), including issues such as foraging mode (sit-and-wait versus active foragers),the presence of competitors (intra and inter specific competition) and the relative abundance and availability of alternative prey species. Dietary specialization may be influenced by individual strategies (Holbrook and Schmitt 1992; Bolnick et al. 2003), foraging experience (Amundsen et al. 1995), sexual dimorphism (Camilleri and Shine 1990), body size (Holbrook and Schmitt 1992; Beaudoin et al. 1999), age, or population density (Svanbäck and Persson 2004). Some of these explanations are specific to particular taxa, but others may apply more broadly. For example, many models of optimal foraging predict whether predators will add or delete prey types from the diet based on energetic efficiencies (cost/benefit ratio; Schoener 1971, Stephens & Krebs 1986). The assumptions underlying many optimal foraging models have attracted strong

criticism (Pierce and Ollason 1987), and arguments based on currencies other than energy intake may prove to be more useful. For example, in many predator taxa, the body size of a predator is strongly linked to the size of its prey (Vézina 1985, Arnold 1997). Based on the near-ubiquity of this relationship among snakes and their prey, Shine and Wall (2007) suggested that the intraspecific range in body sizes of the predatory taxon compared to its prey species will influence dietary diversity. That is, dietary specialization is likely only if the available range of body sizes of prey within a single prey taxon fills the spectrum of prey sizes potentially used by a snake species. If individuals of any given prey species span only a small size range, snake predators likely will be forced to shift from one prey species to another as they grow larger (Shine and Wall 2007).

These arguments suggest that examining ontogenetic shifts in prey types and sizes within predator taxa may yield insights into the determinants of dietary diversity. That is, as a predator grows larger it can increase its prey size in one of two ways: either by taking larger specimens of the same prey species, or by shifting from one prey species to another. The former route produces dietary specialization, whereas the latter results in a generalist diet. What factors determine which of these two pathways is followed? Ideally, a model system to explore this question would involve a comparison between predator-prey systems that are similar in most important respects. For example, (a) closely related species of predators exhibiting similar ranges in body sizes (so that biomechanical and ecological comparisons are not weakened by interspecific divergence in other traits); (b) sympatric predators, so that general ecological conditions are held constant; (c) gape-limited predation, to generate a simple unambiguous causal link between predator size and maximum ingestible prey size; (d) predators that consume relatively large prey, thus amplifying the effects of variation in predator body size on the range of ingestible prey (Shine and Wall 2007); and (e) a limited morphological diversity in prey taxa (simplifying quantification of "prey size" in terms of nutritional benefit and gape-limitation: Vincent et al. 2004). Lastly, we need dietary divergence between our

predators, accompanied by divergence in the range of body sizes within prey taxa (i.e., one predator species has access to prey of a wide size range within a single prey species, whereas the other predator species takes prey taxa that each encompass only limited intraspecific size variation).

The amphibious sea snakes (sea kraits) of the Great Lagoon of New Caledonia fulfil all of these conditions. In the course of ecological research on insular populations of these snakes, we found that one taxon has a relatively specialized diet (> 45% of prey items belong to a single taxon) whereas the other feeds more broadly (no single species constitutes > 25% of prey recorded). We have thus examined ontogenetic shifts in diet of both taxa, to explore the hypothesis that interspecific divergence in the degree of dietary specialization can be explained by relative magnitudes of body-size variation in predators compared to their prey.

2 MATERIAL AND METHODS

2.1 Study species and sites

Two sympatric species of sea-kraits are abundant in New Caledonia: *Laticauda saintgironsi* (Cogger and Heatwole, 2006) and *L. laticaudata* (Saint Girons 1964; Ineich and Laboute 2002). Neo-Caledonian sea-kraits forage in the lagoon where they feed on more than 50 species of fishes, mostly anguilliform taxa (moray-eels, snake-eels and conger-eels; Ineich et al. 2007). The snakes forage along the lagoon floor, exploring cavities and burrows in search of sheltering fish. After a successful foraging trip that generally lasts about one week, the snakes return to land for one to two weeks to digest their prey (Heatwole 1999; Shetty and Shine 2002b; Brischoux & Bonnet 2007). During a long-term field study, we monitored snake populations on islets in the southwest lagoon (from north to south: Tenia, Mba, Signal, Larégnère, Amédée, Porc-Epic, Nouaré, Bayonnaise, Brosse). Since 2002, we have captured by hand and uniquely marked (scale-clipped) 4,714 individuals (2,553 *L. saintgironsi* and 2,161 *L. laticaudata*). Each snake was measured (snout vent length-

SVL, ±1cm), and weighed (±1g). The two species overlap greatly in body sizes, with SVL ranges of 33.5 to 120.0 cm in *L. saintgironsi* and 38.0 to 137.0 cm in *L. laticaudata*. Further details on our procedures are available elsewhere (Brischoux & Bonnet 2007; Brischoux et al. 2007b).

We classified snakes smaller than 50 cm in SVL as young-of-the-year (based on growth rates from 4,200 recaptures of marked individuals). From field observations (the smallest male engaged in courtship and the smallest female with vitellogenic follicles, as detected by palpation), we identified the minimal snout vent length at maturity as 75.5 cm (female) and 63.0 cm (male) for *L. saintgironsi*, and 88.5 cm (female) and 70.0 cm (male) for *L. laticaudata*. Snakes greater than 50 cm in length, but less than adult size, were classed as juveniles. 2002]).

2.2 Composition of the diet

The abdomen of each captured snake was palpated to detect the presence of a prey in the stomach; any items detected were gently pushed out the snake's mouth for identification and measurement. Sea-kraits feed mostly on non-spiny anguilliform fishes, easily regurgitated without risk of injury for the snake. Regurgitated prey were weighed, measured (total length and maximum midbody diameter) and later identified based on their dentition and other morphological traits (Böhlke et al. 1999; Smith 1999a, 1999b; Smith and McCosker 1999; Brischoux et al. 2007a). Previous analysis showed a low dietary overlap between the two sea krait species (Morisita-Horn similarity index of 0.15) and a strong contrast in their respective foraging habitats (hard bottoms for *L. saintgironsi* versus soft bottoms for *L. laticaudata*: Brischoux et al. 2007b). Despite a strong dietary divergence, the two taxa do overlap in terms of some of the prey species consumed, suggesting a broad similarity in foraging tactics (Brischoux et al. 2007b). We allocated each eel species to a habitat type (hard, soft, or hard-plus-soft substrates) based on information in FishBase (Froese and Pauly 2006).

2.3 Analyses

We performed richness estimates to test the effectiveness of our sampling of snake diets (Chao estimator, Colwell 2005). We calculated similarity indexes (Morisita-Horn index: Magurran 1988, 2004) to quantify dietary overlap between the three age classes (young-of-the-year, juveniles and adults) within each species. The analyses were performed using Estimates 7.5 (Colwell 2005), and Statistica 7.1 (Statsoft 1984-2005).

3 Results

3.1 Morphology of prey

Body sizes and shapes differed between eels from hard-bottom *versus* soft-bottom habitats. Eels from hard coral tended to be much stouter-bodied than mud-burrowing species. Thus, ANOVA with habitat category (hard, hard plus soft, soft) as the factor, and prey dimensions as the dependent variables, showed that eels from hard-coral areas averaged shorter (prey length: $F_{2,666}$ = 16.82, P<0.0001) but were thicker-bodied (prey diameter: $F_{2,397}$ = 13.95, P <0.0001) than eels from soft-bottom habitats (all posthoc tests P<0.05). Importantly for the critical issue of variation in body sizes within prey taxa, coefficients of variation of prey diameter averaged significantly lower for eel species from soft-bottom habitats (n=3 prey species with suitably large sample sizes, mean ± SD = 0.15 ± 0.02) than for eel species from hard-coral habitats (n=10 prey species, mean=0.26 ± 0.07; $F_{1,11}$ = 5.76, P<0.04).

In summary, eel species from soft-bottom areas of the Lagoon tended to be long but slender-bodied, with each species typically covering only a small range of body sizes. In contrast, eels from hard-coral habitats tended to be thicker-bodied; and the range of body sizes within each species tended to be higher than for the mud-dwelling anguilliform taxa.

3.2 Interspecific and age-related differences in dietary diversity

We collected more prey items in *L. saintgironsi* (N=655; 34 prey species) than in *L. laticaudata* (N=365; 28 prey species), but the richness estimators in both species plateaued after a sample size of 250 prey items, indicating that our sampling was adequate to quantify prey diversity (Colwell 2005).

In *L. saintgironsi*, dietary composition changed little among age classes. Similarity indices were high for comparisons between young-of-the year and juveniles (0.94), and between juveniles and adults (0.91). That is, all individuals of this species tended to feed on the same prey species throughout their life. One moray-eel species (*Gymnothorax chilospilus*) comprised about half of all prey items found in this species; no other prey species comprised more than 9% of the diet (Table 1). Although detailed analysis suggests an increasing diet diversity with snake growth (2 eel species among 13 were eaten exclusively by young-of-the-year; 2 among 21 by the juveniles; and 13 among 30 by the adults), the prey taxa involved in this ontogenetic shift were minor components (< 6%) of the overall diet.

In contrast, *L. laticaudata* age classes differed significantly in diet (similarity indices 0.70 between young-of-the-year and juveniles, and 0.24 between juveniles and adults). At least three prey species constituted > 10% of the diet for each age class of predators (Table 1), with the identity of these dominant species shifting among predator age classes. For example, although young-of-the-year often fed on *Myrophis microchir* (38% of prey items), this species represented only 10% of the diet of juvenile snakes, and 1% for adults. Similarly, *Anarchias allardicei* represented 16% of the diet of juvenile snakes, but was never recorded in neonates or adults. Interestingly, the main prey species of *L. saintgironsi* (*G. chilopsilus*) also occurred (albeit, much less commonly) in the diet of *L. laticaudata* (Table 1).

TABLE 1 - *List of the fish species identified from sea kraits stomach contents, with their percentage in each diet (*L. laticaudata *and* L. saintgironsi*, LL and LS respectively). Sample sizes were N=365 prey items for* L. laticaudata *and N=655 for* L. saintgironsi*. Habitats were extracted from FishBase (Froese & Pauly 2006). Species in bold comprise more than 10% of the sea krait diets.*

Species	Neonates		Juveniles		Adults	
L. saintgironsi	***G. chilospilus***	48.5%	***G. chilospilus***	51.1%	***G. chilospilus***	44.4%
	12 sp.	51.5%	20 sp.	48.9%	29 sp.	55.6%
L. laticaudata	***M. microchir***	37.5%	*Conger sp.*	25.0%	***G. albimarginatus***	28.0%
	Muraenichthys. sp.	30.0%	*Muraenichthys. sp.*	16.4%	*Conger sp.*	23.4%
	Conger sp.	15.0%	*A. allardicei*	15.4%	*G. moluccensis*	13.5%
	G. chilospilus	10.0%	*G. albimarginatus*	14.5%		
			M. microchir	10.0%		
	2 sp.	7.5%	11 sp.	18.7%	19 sp.	35.1%

In summary, one of the sea krait species (*L. saintgironsi*) took a relatively narrow range of prey taxa, and showed little ontogenetic shift in diet. The other sea krait (*L. laticaudata*) took a wider range of prey types, and these shifted with age class within the predator population.

3.3 Prey size

The most critical dimension of prey size for gape-limited predators such as snakes is likely to be maximum prey diameter. Accordingly, our analyses use this measure of prey size. As expected in gape-limited predators, larger snakes tended to feed on larger prey items (*L. saintgironsi* r^2=0.45, N=536, p<0.001; *L. laticaudata* r^2=0.48, N=228, P<0.001). This pattern is driven at least partly by gape-limitation, because the largest prey items (e.g., an eel > 76 cm long) clearly could not be physically ingested by a neonate (< 50 cm SVL) snake. Positive correlations between prey size and snake SVL were evident within as well as among prey species (e.g., r^2=0.14, N=238, p<0.001 using *Gymnothorax chilospilus* for *L. saintgironsi*; r^2=0.67, N=46, p<0.001 using *Conger. sp.* for *L. laticaudata*). However, the ontogenetic

increase in prey size was also achieved by the incorporation of larger prey species in the diet of larger snakes (Table 1, Figure 1).

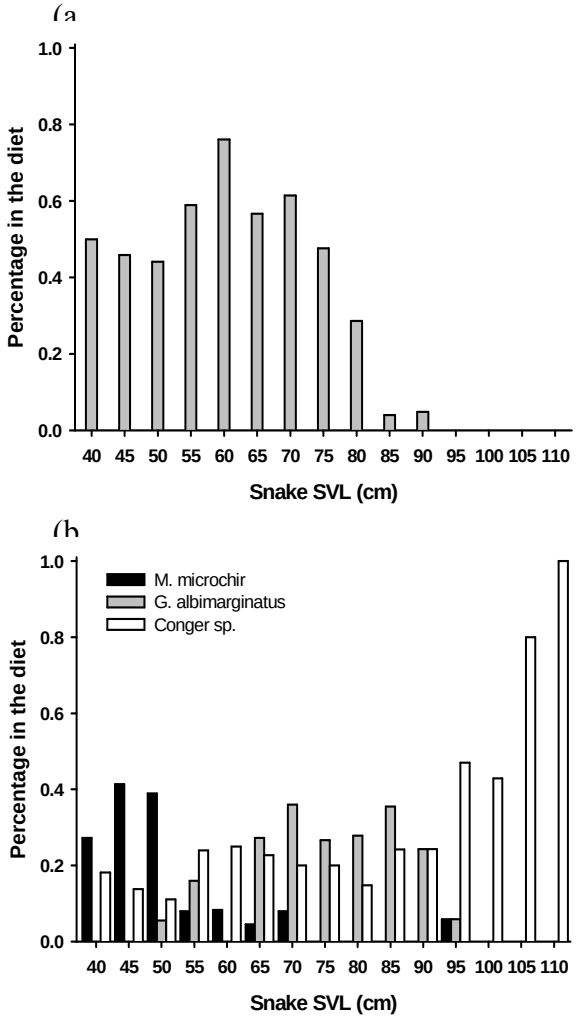

FIG. 1 - *Size-related shifts in taxonomic composition of the diet in sea kraits (*Laticauda *spp.). The Figure shows the proportion of the main prey species eaten by 10 cm size classes of snakes, for each of the two* Laticauda *species: (a) in the hard-coral specialist* L. saintgironsi*, the single eel species* Gymnothorax chilospilus *spans a wide size range and hence is the main prey species for each age class; (b) in contrast, the soft-bottom eel species taken by* L. laticaudata *typically span a smaller size range and hence each is taken by a different size class of predator (and thus,* Myrophis microchir, G. albimarginatus *and* Conger *sp. are the main prey species of young-of-the-year, juvenile and adult snakes respectively).*

In summary, larger snakes selected both larger fish (within each prey species) and larger prey species. The two snake species differed in the relative importance of these two mechanisms, however: *L. laticaudata* mostly took different (larger) prey species as they grew larger, whereas *L. saintgironsi* tended to take larger individual prey items but of the same species as they consumed earlier in life (Table 1, Figure 1). The shift in prey size with increasing snake size was more pronounced in *L. saintgironsi* than in *L. laticaudata* (ANCOVA with prey diameter as the dependent variable, snake species as the factor and snake SVL as the covariate: difference between the slopes $F_{1,760}$=10.16, P=0.001). In neonates, the length of the prey relative to the SVL of the snakes averaged 54.0±1.6% and 41.1±0.7% in *L. laticaudata* and *L. saintgironsi* respectively; but these values were 36.7±1.2% and 38.1±1.2% in the adults, revealing that *L. saintgironsi* increased the size of its prey more steeply during growth. Overall, then, *L. saintgironsi* displayed a weak ontogenetic shift in prey taxonomic identity combined with a steep ontogenetic increase in prey size, whereas *L. laticaudata* exhibited the reverse trend.

Reflecting these patterns, prey size (diameter) relative to snake body length showed clear divergences between snake species and between eels from different types of habitats. Reflecting the more elongate bodies of soft-bottom eels (see above), these animals were thinner relative to the snakes that had consumed them ANCOVA with prey diameter as dependent variable, eel habitat type as the factor, snake SVL as covariate,: $F_{2,632}$=34.04, P<0.001; posthoc tests have soft versus hard-bottom eels different at $P < 0.05$, Figure 2). Interestingly, the correlation between prey size and predator size also was higher for soft-bottom eels (using absolute values of the residual scores from the general linear regression of prey size versus snake size as the measure of tightness of correlation: $F_{2,633} = 4.57$, $P < 0.015$; posthoc tests show soft-bottom eels significantly lower than either of the other habitat categories).

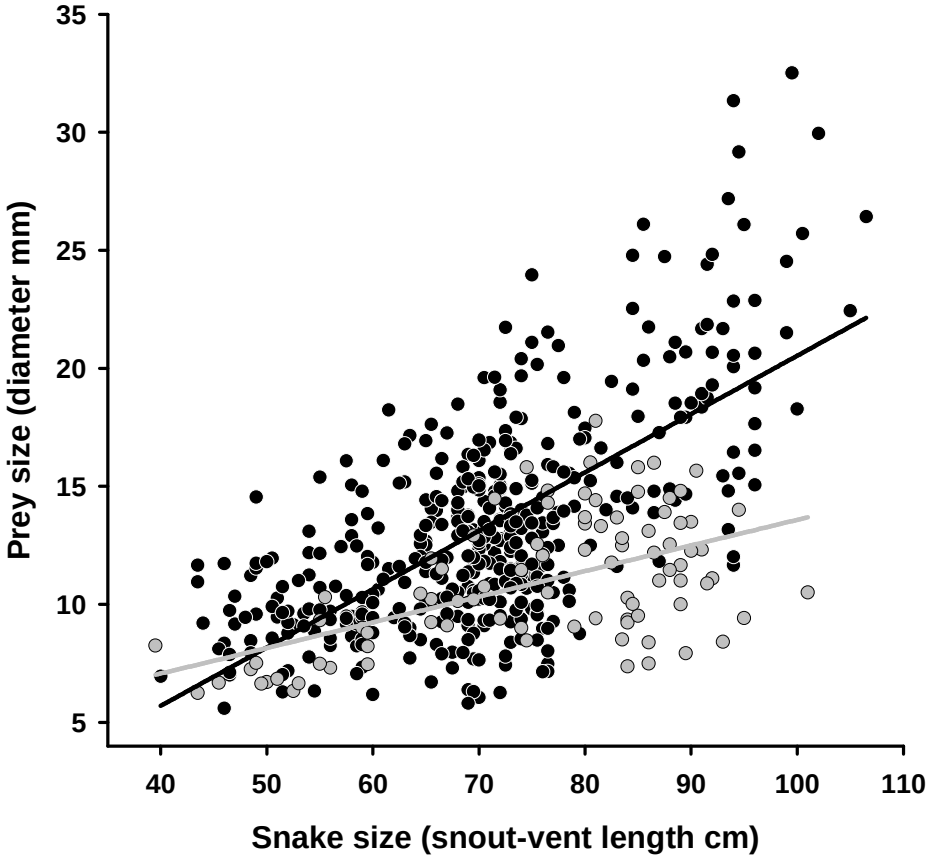

FIG. 2 - *Relationship between snake size and prey diameter for prey taxa living in different types of habitat. Grey circles (grey regression line) for soft-bottom eels) and black circles (black regression line) for hard-substrate eels. Soft-bottom eels were thinner relative to the snakes that had consumed them.*

3.4 Direction of prey ingestion

The degree of size-matching between anguilliform fishes and their crevices is lower in hard-coral areas than in eels from soft-bottom areas, because the former use existing (variably-sized) retreats whereas the latter excavate their own burrows. Thus, a snake seizing an eel in a hard-coral matrix may have more room to move, and be able to seize the eel at any part of its body. In contrast, a snake entering a

burrow in soft-bottom areas will be likely to encounter (and thus, seize and swallow) the eel head-first. As predicted, *L. saintgironsi* seized and swallowed prey randomly with respect to direction (51% head first, N=450) whereas *L. laticaudata* swallowed head first most of the time (83% head first, N=210; χ^2=62.8, p<0.001).

Overall, then, both snake species took larger prey items as they grew older, but did so via different pathways. *Laticauda saintgironsi* tended to take larger individuals of the same prey species, whereas *L. laticaudata* shifted to different (larger) prey species. Prey size was more tightly linked to predator body size in *L. laticaudata* than in *L. saintgironsi*.

4 Discussion

Our field data document both strong similarities, and major divergences, in the trophic ecology of these two sympatric, congeneric sea snakes. Both feed almost entirely on anguilliform fishes, which they obtain by entering the crevices and burrows in which the eels live (Abrams et al. 1982; Ineich et al. 2007). Although the two snake taxa attain very similar body sizes, and return to the same islets to digest their prey after foraging trips, they obtain their prey from different habitats within the Lagoon. Most of the eels taken by *L. saintgironsi* are obtained from among the interstices of hard coral, whereas many of the prey of *L. laticaudata* are taken from burrows in muddy (soft-bottom) areas (Brischoux et al. 2007b). That difference in foraging sites offers a plausible starting point for a sequence of events that ultimately cause divergence in dietary breadth between the two predator species.

Critically, eels from soft-bottom habitats are subject to biomechanical constraints on burrowing (these fishes must dig their own burrows, unlike the hard-coral eels) and constraints on maximal burrow diameter imposed by physical properties of the substrate (i.e., too large a burrow will collapse, Woolnough and Steele 2001). This situation generates important differences between burrowing eels and hard-coral

eels. First, the burrowing eels tend to be relatively long and thin. Second, the range of body sizes within each species is smaller than in hard-coral taxa (perhaps reflecting specialization for particular substrate types). Third, eels are size-matched to their own burrows, so that any snake attempting to penetrate the burrow can be only marginally thicker than the eel inside. In combination, these factors generate a situation where *L. laticaudata* takes a wide range of prey species overall (although a narrow range within any given age class of snakes) and where prey size is highly correlated with predator size. In contrast, the eels taken by *L. saintgironsi* live within the hard-coral matrix, where crevices span an immense range and the eels can simply move to larger crevices as they grow larger. Size-matching of eel to crevice will be weaker, allowing a weaker correlation between prey size and predator size. More importantly, eel species in these habitats can span a wide size range (adjacent crevices are often of very different sizes, allowing easy movement between them), so that an ontogenetic increase in prey size within *L. saintgironsi* can be accomplished by simply taking larger individuals of the same eel species, rather than switching to different (larger) species. The divergence in the proportion of prey eaten head first between the two snake species supports the notion that the constraints imposed by the prey shape-prey habitat relationship are relaxed in hard substrates compared to soft bottoms.

Although we lack information on several aspects of the predator-prey relationship in this system (e.g., anti-predator tactics of eels, and the profitability of different prey types), the situation affords a robust comparison because the two predator-prey systems are similar in so many respects except for the habitat use of their prey. Under the hypothesis outlined above, the difference in dietary breadth between these two sympatric snake species ultimately is driven by habitat-imposed differences in constraints on body shape and size of the major prey taxa. Thus, the sea-snakes of the Neo-Caledonian Lagoon may provide an unusually clear example of the cascade of consequences from habitat structure through to prey morphology through to predator dietary diversity.

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LES TRICOTS RAYÉS COMME BIO-INDICATEURS

Anguilliform fishes and sea-kraits: neglected predators in coral-reef ecosystems

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Abstract. Despite intensive sampling efforts in coral reefs, densities and species richness of anguilliform fishes (eels) are difficult to quantify because these fishes evade classical sampling methods such as underwater visual census and rotenone poisoning. An alternative method revealed that in New Caledonia, eels are far more abundant and diverse than previously suspected. We analysed the stomach contents of two species of sea snakes that feed on eels (*Laticauda laticaudata* and *L. saintgironsi*). This technique is feasible because the snakes return to land to digest their prey, and (since they swallow their prey whole) undigested food items are identifiable. The snakes' diet consisted almost entirely (99.6%) of eels and included 14 species previously unrecorded from the area. Very large populations of snakes occur in the study area (e.g., at least 1,500 individuals on a small coral islet). The snakes capture approximately 36,000 eels (972 kg) per year, suggesting that eels and snakes play key roles in the functioning of this reef ecosystem.

KEYWORDS: anguilliform fishes, biodiversity, coral reefs, populations, sampling, sea snakes

1 INTRODUCTION

Coral reef ecosystems are renowned as biodiversity hot spots (Roberts *et al.* 2002), but many are in crisis due to threats such as global warming, over-fishing, and marine pollution (Walker and Ormond 1982, Linden 1999, Hughes *et al.* 2003, Riegl 2003). Such threats are worsening over time (Rogers 1990, Hughes 1994, Guinotte *et al.* 2003, Pandolfi *et al.* 2003, Sheppard 2003, Bellwood *et al.* 2004). To conserve these complex ecological systems, we need to understand how they function. Predation may exert a critical influence on complex ecosystems such as these, by enhancing the stability (resilience) of the whole community (Carpenter *et al.* 1985, McCann *et al.* 1998, Finke and Denno 2004). Unfortunately, some biotic components of these systems are highly cryptic, and hence difficult to sample in any quantitative fashion. For example, moray eels are widespread in tropical oceans but are very secretive and often nocturnal, and hence difficult to sample. Consequently, their actual abundance and diversity remain poorly known (Kulbicki 1997).

We adopted a novel approach to address this problem, using data on feeding rates and prey types of sea kraits (sea snakes from the genus *Laticauda*) that are specialist predators on anguilliform fishes (henceforth named "eels" for simplicity). Sea kraits forage at sea but return to land to digest their prey. The snakes readily regurgitate freshly-ingested prey items, facilitating dietary analysis (Heatwole 1999, Reed *et al.* 2002). High densities of sea kraits occur in many areas of the western Pacific Ocean (Heatwole 1999). Since 2002, we have been conducting ecological studies on two species of sea kraits within the New Caledonia lagoon, providing an extensive data-set on the eels consumed by these snakes. To compare our results to those from other methods of surveying eel populations, we have taken advantage of long-term surveys conducted to assess fish communities in the same region (Kulbicki 1997). Thus, these two large data-sets provide a robust opportunity to compare results obtained from classical sampling methods *versus* analyses of predator (snake) stomach contents. We specifically addressed the following issues:

The densities and species diversity of the eel fauna, as assessed by classical sampling techniques (underwater visual censuses and rotenone poisoning)

The densities and species diversity of the eel fauna, as assessed by forced regurgitation of snake stomach contents

The rate of prey consumption by sea kraits, and hence the overall offtake of eels by these marine predators

2 MATERIAL AND METHODS

2.1 Underwater surveys

The relative abundance and diversity of fish communities have been assessed in various reef ecosystems across the South Pacific Ocean, primarily based on underwater visual censuses but also (to a lesser extent) using rotenone, fishing lines, trawls, and gill nets (e.g. Jennings and Polunin 1995, Kulbicki 1997, Samoilys and Carlos 2000, Willis 2001, Letourneur *et al.* 2000, Kulbicki *et al.* 2000). For the current study, we used data from transects (based on underwater visual censuses [=UVC]) and rotenone poisoning stations. The UVCs were performed in a radius of 40 km around the snake sampling area (Signal island). All rotenone stations were performed in the southwest lagoon within a 20 km radius of Signal Island. Within this area, the topography of the lagoon is well known (see http://www.shom.fr/ for precise maps of the area). The lagoon is approximately 15-20 km wide between the mainland and the barrier reef. The bottom is relatively flat, ranging between 10-29m in depth, and slightly deeper toward the mainland. Two narrow passes (facing two rivers) open the external barrier and stretch from the drop-off to the lagoon for a distance of roughly 10 km with a maximal depth of 70m. Thirty reef flats (0-15m deep; 17 of them with small islets <10 ha) are scattered in this area of the lagoon. The drop-off is very steep: one km into the open sea the depths is greater than 150m, and quickly reaches 800m. Our surveys were performed on shallow reefs, easily accessible by the divers (0-30m); thus, the passes and the deep drop-off were not

sampled. Other parts of the neo-Caledonian lagoon are similar to our own study area in terms of depths, reef flats and drop-offs (maps available from http://www.shom.fr/).

Underwater visual censuses (UVC) - This is the most popular method for surveying fish communities. The UVC surveys were performed by counting the fish observed along a 50 m transect by two divers, one on each side of the transect. For each sighting, the species and its estimated body length were recorded together with the distance of the fish from the transect line. This type of information allows estimates of the density and biomass of each species encountered (Buckland et al. 1993). A total of 1592 transects were performed on an array of reef types (Table 1 and 2). Transects were performed using distance sampling with no distance constraint (Buckland et al. 2001). In other words, the observers noted all the fish they could see, recording the distance of each observation from the transect line. Most of the fish were observed within the first 5 m. The duration of a transect survey depended on fish density, ranging between 75 and 90 minutes. The mass of the fish was estimated using mass/length data obtained on freshly caught specimens measured in the laboratory (Kulbicki 1988; Kulbicki and Wantiez, 1990; Kulbicki et al. 2005). We estimated densities and biomasses of fish using algorithms developed by Kulbicki and Sarramégna (1999). Previous studies have indicated that the precision of length estimates is usually within 15% when mixing several species, and 5% when working on single species (Harvey et al. 2000).

Rotenone poisoning - The rotenone poisoning sessions were performed by enclosing 300 m^2 of reef with a fine mesh net (1 cm stretched mesh) reaching from the bottom to the surface, then releasing 5 kg of rotenone powder (10% active ingredient) mixed with seawater and liquid soap. On each rotenone station, 4 divers deployed a 60m circular net. This net had a 1 cm stretched mesh in order to prevent the escape of small fish, and was secured to the sea floor. Once the net was set, each diver dispersed 3 liters of rotenone paste. A total of 8 dm^3 of powder was used on each station. The fish died within five minutes and were collected by the divers,

helped by four people on the surface. The entire catch was brought to the laboratory; each specimen was later identified, measured and weighed, allowing estimation of density and biomass per species. The densities of eels obtained from rotenone sampling were estimated by dividing the number of fish by the surface sampled (N/300m²). A total of 57 rotenone collections were performed in the southwest lagoon of New Caledonia between 1986 and 2003. The rotenone data were already available before we undertook fish sampling using sea kraits. Thus, for the comparative purposes of the current study, we simply used previously collected samples.

2.2 Fish sampling via sea kraits

Sea krait ecology - Sea kraits (Elapidae, Hydrophiinae) are large (to 1.5 metres) venomous sea snakes that forage in the ocean, mostly on eels, and return to land to digest their prey (Heatwole 1999). Consequently, many of the snakes found on land contain prey in the stomach. Sea kraits also come on land to slough their skins, to reproduce (for mating and egg-laying), and possibly for other reasons (e.g. resting, recovering from injuries: Shetty and Shine 2002b). These snakes are active foragers and by virtue of their elongate bodies and small heads, are able to penetrate deep into the coral matrix to locate and extract eels hidden within these complex structures. Although many authors have mentioned that sea kraits are abundant throughout the Pacific, there are few data on their population densities, and thus, their ecological role remains poorly understood.

Studies on sea kraits in Fiji and Vanuatu have shown that these animals are highly philopatric (Shetty and Shine 2002a), that they feed on eels (Reed *et al.* 2002, Shetty and Shine 2002d), and that they require about one week to fully digest a large eel (Shetty and Shine 2002b). Two species of sea-kraits occur in New Caledonia: *Laticauda saintgironsi* (formerly regarded as part of the wide-ranging *L. colubrina*: Cogger and Heatwole 2005, Heatwole *et al.* 2005) and *L. laticaudata* (Saint Girons 1964, Ineich and Laboute 2002).

Population size - On Signal Island (a 6-hectare flat islet situated in the southwest lagoon of New Caledonia, 15 km west of Nouméa and 10km from the external reef barrier; 22°17'45.93 S; 166°17'34.70 E) we individually marked (by scale-clipping) more than 1,000 individuals of these two snake species (*L. saintgironsi*, N=424, and *L. laticaudata*, N=579) during three field trips, from November 2002 to March 2004. Each year, we (one to three people) performed three standardized surveys per day (30 minutes to 1 hour in duration, one early in the morning, one at dusk and one at night). This timing encompasses the most intense terrestrial activity of the snakes. We patrolled a 450m section of the shore comprising flat beach rocks (80%) and small sandy beaches (20%). The snakes are primarily restricted to this southwestern part of the islet (unpublished data). The total number of searching days was 41. For each snake, we recorded snout-vent length (± 1 cm) and body mass (± 1 g, with an electronic scale). We obtained 420 recaptures of marked snakes (90 for *L. saintgironsi*, 330 for *L. laticaudata*) and estimated population sizes of snakes from these mark-recapture data using the CAPTURE program (Otis *et al.* 1978, Bonnet and Naulleau 1996, Bonnet *et al.* 2002c).

Diet - We focused on relatively intact (recently-ingested) prey items, as we forced snakes to regurgitate (through gentle palpation) only when we estimated from initial palpation that the prey was firm and hence, not yet digested. We weighed each prey item and preserved it for later identification, primarily based on dentition, at the MNHN laboratory. Sea kraits swallow their prey whole, either tail or head first. In many cases of head-first digestion, the eel's head was already partly digested by the time that we captured the snake and thus, dental characters were missing from the prey item. Overall, we were able to confidently identify only 18.8% of the total number of prey items regurgitated by our snakes.

Because the consumed eels are very large relative to the snakes that eat them, and the snake's body wall is very thin compared to the diameter of the fish, it was often possible to measure the diameter of the prey in the snake's stomach *in situ* (see Shine and Sun, 2003 for validation of this method), except when the prey was too

digested and became soft during palpation. In this way we could obtain data on prey size without unnecessarily stressing the snake or depriving it of its prey.

We identified 105 regurgitated prey items, and measured diameters of 271 prey. Data on the mass and the midbody diameter of regurgitated, freshly ingested prey allowed us to characterise the relationship between prey diameter *versus* prey mass (*log Mass prey (g) = 1.88 log (Diameter of Prey (mm)) - 2.00*; r = 0.81, $F_{1, 82} = 154.2$, $P < 0.0001$). From this relationship, we estimated the mass of prey items for which we had only midbody diameter measurements (because they were measured *in situ*, or were regurgitated but were too fully digested to be weighed). Using this prey diameter/prey mass relationship, we could also quantify the size distribution of ingested eels, and then extrapolate that distribution to estimate the number of prey items of different body sizes that are taken by the Signal snakes every year.

Duration of digestion - To estimate feeding rates, we needed data not only on the proportion of snakes with freshly captured prey, but also on the duration of digestion. From recapture data within survey periods, we could assess the time required for a snake to digest a prey (i.e., the minimum time elapsed between the capture of a snake with a recently ingested prey and its recapture with an empty stomach).

Foraging trip duration – In the same way, we could assess the time required for a snake to undertake a successful foraging trip. We used the time elapsed between successive captures on individual snakes that were first caught when leaving the island (captured on the beach while moving toward the sea) with an empty stomach, and then recaptured when coming back on land to digest (i.e., hauling onto the beach with a full stomach).

3 Results

3.1 Estimating the abundance of eels using underwater surveys

TABLE 1- *Underwater visual census (UVC) surveys in various sites of the southwestern New Caledonia lagoon suggest a very low density of eels. Size (total length, cm) and mass (g) represent the mean (±SD) estimated body size and body mass of the eels. UVC samples mostly comprised very large fishes.*

Site	# of transects	# of eels sighted	Eels/m²	# of eels species	Mean eels length (cm)	Mean eels mass (g)
Noumea-1	90	7	0.00052	6	53±30	148
Noumea-2	108	1	0.00006	1	30	34
Barrier Reef	330	12	0.00017	4	86±30	527
South West	800	29	0.00019	5	79±25	431
St Vincent Bay	72	9	0.00052	3	91±22	618
Algae-beds	192	4	0.00014	3	45±10	97

TABLE 2- *A comparison of three methods for estimating population densities of eels (Congridae, Muraenesocidae, Muraenidae, and Ophichthidae) in the New Caledonia lagoon. UVC = underwater visual survey.*

Sampling technique	Sampling period	Sampling effort: # days	# of eels sampled	# of species detected
UVC	1996-2001	1,323	85	8
Rotenone	1986-2003	57	247	29
Sea snakes	2002-2004	56	354	47

Underwater visual census – Results from this technique suggested that eels are rare: we found a mean density of only 4.6 ± 2.8 eels/ha (data shown are mean ± SD, in this all subsequent results; ranging from 0.6 to 5.2 fish/ha; Table 1). Despite a massive survey effort, UVCs detected only 8 of the 95 eel species known to occur in New Caledonia (Table 2, 3). The eels recorded during visual census surveys were generally very large (mean mass 438±306g), with few individuals less than 100g and none under 10g (Fig. 1).

TABLE 3 - *List of the fish species seen during underwater visual surveys (UVCs) in the SW lagoon of New Caledonia, caught by rotenone in the SW lagoon, or prey found and identified in the stomach of the sea kraits. Status (for prey only): already known for New Caledonia (e.g. MNHN collection…), versus first report for the area.*

Family	Species	Status	UVC	Rotenone	Snakes
Moringuidae	*Moringua ferruginea*			X	
Xenocongridae	*Kaupichthys diodontus*			X	
Muraenidae	*Anarchias allardicei*	First report			X
	Anarchias sp.	Known			X
	Echidna nebulosa		X		
	Echidna polyzona			X	
	Echidna sp.	Known			X
	Echidna unicolor	First report			X
	Enchelycore bayeri			X	
	Enchelycore pardalis	First report			X
	Gymnomuraena zebra			X	
	Gymnothorax australicola	First report			X
	G. albimarginatus	Known	X	X	X
	G. buroenis	Known		X	X
	G. chilospilus	Known		X	X
	G. cribroris	First report			X
	G. dorsalis	First report			X
	G. eurostus	Known		X	X
	G. favagineus	First report			X
	G. fimbriatus	Known		X	X
	G. flavimarginatus		X	X	
	G. fuscomaculatus	Known		X	X
	G. gracilicauda	First report			X
	G. javanicus		X	X	
	G. meleagris	Known	X	X	X
	G. melatremus			X	
	G. moluccensis	First report			X
	G. monochorous	Known		X	X
	G. margaritophorus	Known		X	X
	G. nudivomer	Known		X	X
	G. pindae	Known		X	X
	G. pseudothyrsoideus	Known		X	X
	G. reevesi	First report			X
	G. reticularis	First report			X
	G. richardsoni	Known		X	X
	Gymnothorax sp.	Known			X
	G. undulatus	Known		X	X

Family	Species	Status	UVC	Rotenone	Snakes
	G. schizomatorhynchus			X	
	G. zonipectis	Known		X	X
	Scuticaria tigrina	Known			X
	Scuticaria okinawae	Known			X
	Siderea picta		X		
	S. thyrsoidea		X	X	
	Stophidon sathete	Known			X
	Uropterygius alboguttatus	First report			X
	U. concolor	Known			X
	U. fuscoguttatus	Known			X
	U. macrocephalus	First report			X
	Uropterygius sp.	Known			X
	U. cf. xanthospilus	Known			X
Ophichthidae	*Leiuranus semicinctus*			X	
	Muraenichthys sp.	Known			X
	Myrophis microchir	First report			X
	Myrichthys maculosus	Known			X
	Ophichthus cephalozona			X	
	Ophichthus sp.	Known			X
	Schismorhynchus labialis	Known			X
Congridae	*Conger cinereus*	Known	X	X	X
Microdesmidae	*Ptereleotris sp.*	Known			X
Plotosidae	*Plotosus lineatus*	Known	X	X	X

Rotenone poisoning – This method revealed many smaller eels, higher species diversity, and higher population densities of anguilliform fishes than were observed during UVCs (Table 2, 3). The mean density of eels from the rotenone stations was 180 eels/ha (N=57 stations). A total of 45 eels were caught, with an average body mass (91g) one-quarter that recorded during visual surveys (Fig. 1).

The average density of eels estimated using rotenone was 180 fish/ha, 40 times greater than the density suggested by UVCs (4.6 fish/ha). However the mean density of large eels (heavier than 100g) revealed by rotenone poisoning was only 4.6 times greater than that revealed by UVCs (18 fish/ha vs 3.9 fish/ha). The total eel biomass estimated using rotenone (1.27 g/m²) was five times that based upon UVC data (0.25 g/m²); this difference dropped to 3-fold, however, when restricted to data on the largest fish (>100g) (0.70g/m² for rotenone, 0.23g/m² for UVCs).

Thus, UVC surveys clearly generated unrealistically low estimates of eel numbers, and were highly biased toward large individuals.

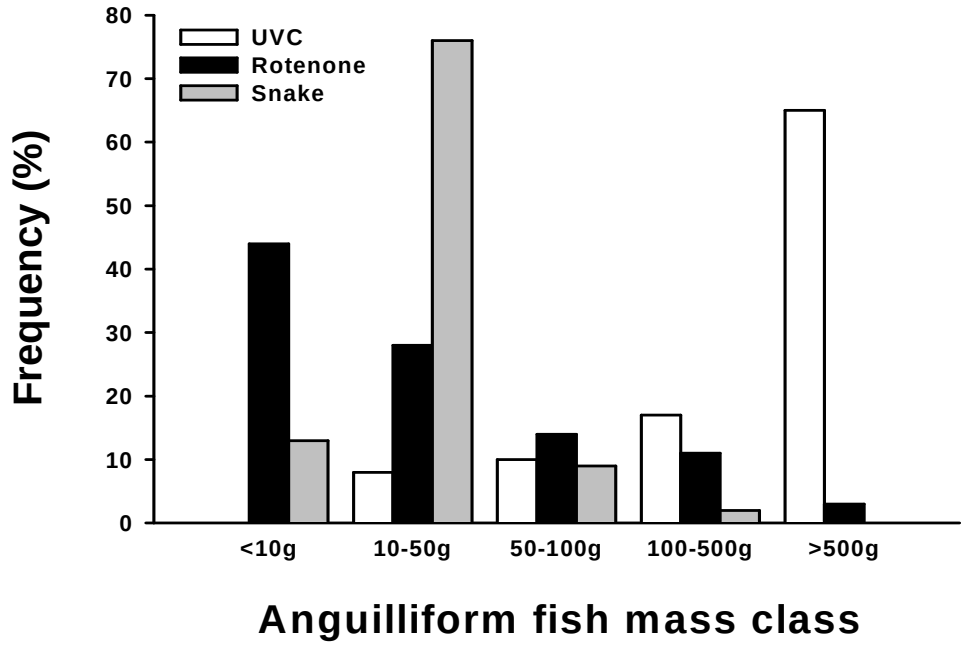

FIG. 1 - *Size (body mass) frequency distributions of anguilliform fishes caught by rotenone (N= 241), observed by underwater visual surveys ([=UVC], N=64), or eaten by snakes (N=331).*

3.2 Population size of sea kraits

Based on rates of recapture of marked animals, Signal Island supported an average of 1,418 individual snakes (estimates for each field trip ranged from 1,095±212 to 1,921±449, extreme values ranging from 771 to 3071). This figure is likely to be an underestimate because although we marked more than 1,000 individuals, the proportion of unmarked snakes remained high throughout our study (68.2 ± 20.9%). We were able to process (mark, measure) only about 100

snakes/day, so could sample only a fraction of the total number of snakes that were visible on the beach.

3.3 Duration of digestion

Prey were detectable by palpation for 6.0±3.1 days (range: 3-12 days, N=15). Therefore, ingested prey are detectable for about a week in free-ranging snakes, in agreement with data from captive Fijian sea kraits (Shetty and Shine 2002b).

3.4 Foraging trip duration

Successful foraging trips lasted generally about a week (6.6 ± 4.0 days, range: 1-16 days, N=32).

3.5 Number and size of eels consumed by snakes

Approximately one-third of the snakes contained prey at capture (33.7%). Because they take one week to digest their prey, and feed all year round (based on our fieldwork in all seasons), we estimated that the snakes on Signal consume a total of about 36,000 eels per year. That is, if each snake feeds once every two weeks (one week to forage, one week to digest), it will take an average of 26 prey items per year. Thus, the 1,418 snakes on Signal will consume 1,418*26 = 36,868 anguilliform fishes.

The mean mass of intact prey items was 38.6±34.3g (N=84). The mean estimated mass of partly-digested prey (based on midbody diameter) was 27.3±18.5g (N=311) (comparing these two values: t-test, P=0.07, using Ln-transformed data to meet the normality assumption). A t-test for paired samples suggests that our use of the prey-diameter *versus* prey-mass regression to calculate prey mass was relatively accurate (comparing the actual mass with the estimated mass of each intact fish: $t<0.001$, N=84, P=0.99, using Ln-transformed data to meet the normality assumption). The slightly (although not significantly) greater mean mass of regurgitated prey items than partly-digested prey items probably reflects the more rapid digestion of smaller prey, thus reducing sample sizes for intact small prey items and biasing our

sample of intact fishes toward larger specimens. Consequently, we used the more conservative (and likely, more realistic) estimated mean value (derived from 311 diameter measurements of partly-digested prey items) to calculate the total biomass of the offtake. Calculated on this basis, we estimate that the snakes from Signal Island consume about 972 kg (36,868 prey items x 27g) of eels every year.

Performing the above estimates separately for each year of the study and using either maximal or minimal values for each parameter used (e.g. population size, mean eel mass) provides a way to evaluate the likely level of error in this analysis. The minimal estimated number of eels captured by the snakes was 20,046, the maximal number was 79,846; in terms of biomass the values ranged between 541 kg and 3,082kg of eels consumed per year.

3.6 Comparisons with fish surveys

Species diversity – Fourteen of the eel species that we found in snake stomachs were previously unrecorded in New Caledonia (Table 3). Although our sampling survey was limited in time and space (there are hundreds of small islets in the lagoon of New Caledonia, see http://www.shom.fr/ for precise maps of the area), and identification effort (we focused only on relatively intact prey items) we found a total of 46 fish species in the stomachs of the snakes. Thus, our single sample markedly increases the list of eel species known from this region. Interestingly, we found six species of the genus *Uropterygius* in snake stomachs, but these fish were never detected during UVC or rotenone sessions. A broad survey of the ecological information available on FishBase (http://www.fishbase.org) suggested that the eel species that live hidden in coral crevices or in sand burrows (e.g. *Gymnothorax criboris*, *Strophidon sathete*, *Uropterygius alboguttatus*, *Myrichthys maculosus*) remained inaccessible to classical sampling methods, but were nonetheless captured by sea kraits. In contrast, the fish species detected by all three techniques (e.g. *Plotosus lineatus*, *Gymnothorax albimarginatus*) are known to live in a variety of habitats (e.g. coral reefs, coastal reefs). In FishBase, we found data on the depths where the fish

have been observed for 29 species also consumed by the snakes. On average, the eels sampled by the snakes live at 32.7±28.9m, (range: 0-180m, N=29), and are usually observed between 5m and 60m depth.

Body-size distributions – The fishes captured by snakes had a different body-mass distribution than those caught by rotenone or observed by UVCs (Fig. 1). Clearly, the three sampling methods target different parts of the eel community. Rotenone caught the smallest fish and the number of fish per size class decreased regularly at larger body sizes. Snakes tended to avoid both the smallest and the largest eels, focusing mostly on an intermediate size range: 73% of the eels eaten by the snakes were within the 10-50 g size class. Last, the UVCs sampled only the largest eels (66% were over 500 g), most of them far too large to be ingested by sea kraits. Thus, the component of the fish community assessed by UVC mostly comprised animals that were not available to the snakes as prey.

Fifty-eight percent of the fishes taken by the snakes (6 to 166 g) were within the size range of those captured during rotenone surveys (Fig. 1), but two-thirds of the fish species consumed by the snakes were not sampled by rotenone (Table 3). Overall, only about 14% of the samples from rotenone poisoning overlapped both in body size and species with the prey items taken by the snakes.

Population densities and biomass – Sea snake sampling enabled us to estimate rates of eel consumption, a type of information not directly comparable with the static density estimates generated by the two other methods. However, several points of comparison can be highlighted. Although we do not know the exact area of reef from which the Signal snakes took their prey, this was probably relatively small because many foraging trips are brief (see above), and many snakes hauled on the beach with essentially undigested food items in the stomach (indicating a short travel time). In addition, many of the small prey are probably shallow-water species (lagoon depth around Signal Island rarely exceeds 20m), and sea kraits are highly philopatric (Shetty and Shine 2002a). Finally, we observed snakes capturing moray eels close to the shore (<30m) of Signal Island. Nonetheless, long distance foraging

trips are possible also. Satellite imagery reveals 130 ha of reef within a 1.6 km radius around Signal Island, and no reef beyond this distance up to 4 km. This spatial arrangement suggests that snakes may remove approximately 36,868 fishes/year in this area.

4 Discussion

Even with the use of correction factors, UVCs may not provide an accurate method of sampling secretive fish species such as moray eels (Jennings and Polunin 1995). The present study takes advantage of a novel method of estimating eel species richness and abundance to clarify the nature and magnitude of errors from UVC counts. Our data suggest that UVCs may underestimate the total density of eels by a factor of 40 comparing to rotenone poisoning, and at least by a similar order of magnitude if sea-krait sampling serves as the reference. Rotenone poisoning is generally considered as the most efficient way to catch secretive fish species (Ackerman and Bellwood 2000). However, observations during such trials suggest that eels are often the last species to be affected by rotenone; perhaps because they live in habitats where oxygen levels are low (the reef matrix or in the sand), they might tolerate low oxygen levels and hence be able to resist the anti-oxygen effects of the poison. Thus, some eels may survive a rotenone poisoning session, or die within the reef matrix or in the sand where they cannot be recovered.

The offtake rates of sea kraits suggest that eels, especially small moray eels, are more abundant and diverse in the New Caledonian lagoon than would be suspected from current methods used to survey marine ecosystems. Many eels, especially small specimens, remain hidden within the matrix of the coral edifices and escape observation. Sea kraits can penetrate deep into the interstices of coral substrates, and thus extract eels from situations in which they would otherwise remain invisible. Although we cannot directly extrapolate our results to all coral reefs of the western Pacific, the striking contrast in estimates of eel densities and diversity from different survey methods reinforce Reed *et al.*'s (2002) suggestion that sea-kraits may offer a

powerful and simple sampling method to assess the importance of this little known part of reef fish assemblages. Unless we know the size of the area covered by foraging snakes, however, we can interpret these data only in relatively broad spatial terms. Secondly, the remarkably high numbers of sea kraits plus their specialised diet of eels and high feeding rates suggest that these amphibious snakes may play a significant role in the trophic structure of the lagoon ecosystem. Sea kraits (and thus, presumably, the eels on which they feed) are common throughout New Caledonia (Saint Girons 1964, Ineich and Laboute 2002, Bonnet *et al.* 2005) and much of the Pacific (Pernetta 1977, Heatwole 1999, Shetty and Shine 2002b).

Sea kraits are potentially themselves an abundant food resource (standing-crop biomass of approx. 324 kg of snakes for Signal Island alone) for predators such as sharks, cod, and large moray eels (Ineich and Laboute 2002). Complex food-webs incorporating multiple predatory species on different trophic levels may enhance the resilience of the ecosystems in and around coral reefs (Bellwood *et al.* 2003, Hughes *et al.* 2003). However, to date, eels and sea snakes have not been incorporated into such models (note the recent review by Bellwood *et al.* 2004), probably reflecting the difficulty of sampling these components of the system.

Some of our results about population densities of eels rely upon a series of calculations that embody various estimates (of feeding rates, etc.); errors in any of these estimates will necessarily affect the accuracy of our predictions. Our estimates on snake population size are likely to be accurate as the assumptions for capture-mark-recapture calculations were met: the sedentary behaviour of sea-kraits together with the short time period for each capture-recapture episode means that we can legitimately treat the Signal snakes as a closed population where rates of migration, recruitment and mortality are negligible (Otis *et al.* 1978, Bonnet and Naulleau 1996, Bonnet *et al.* 2002c). In fact, our inability to process all the snakes we encountered suggests that we are more likely to have underestimated rather than overestimated population size, rendering our calculations conservative. We have also assumed that snakes forage mainly on the bottom of the lagoon around the

small islands, searching for prey in depths of 0-60m, and about 30m on average. This inference fits well with available data on the ecology of the eels (FishBase) consumed by the sea kraits (depth records range from 5-60m, 33m on average). Because we observed several snakes catching their prey in the Signal Island reef flat, and recorded some very short successful foraging trips undertaken by the snakes (<1 day), we can be confident that eels are indeed taken from the reef immediately adjacent to the islet. Consequently, the assumption that most preys are taken in the shallow matrix coral and in the soft bottom of the lagoon is realistic. Other estimates are more subject to error. For example, although the sea kraits feed all year, there may well be seasonal fluctuations in the intensity of predation, or in the sizes and types of prey that are taken. Such effects will be opposed by other simplifications in our analysis: for example, we neglected the fact that snakes often regurgitate several prey rather than a single eel. Such complexities will have little overall effect on our main conclusions, because of the great disparity between estimates of eel biomass and diversity from the sea-krait diets *versus* those from other methods. However, one assumption in our calculations is critical in this respect: the total area over which the snakes forage. It remains possible that some snakes travel much further and deeper than we have inferred, and if this behaviour were common, our density estimates would need to be revised downwards (unless sea kraits from other island populations travel to forage around Signal Island, thus cancelling out any such effect). Importantly, this uncertainty does not alter the fact that eels and sea snakes are far more abundant than previously thought, and hence may contribute significantly to the ecological functioning of the coral-reef ecosystem.

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First record of *Cirrimaxilla formosa* (Teleostei: Muraenidae) from New Caledonia, found in sea snake stomach contents

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RÉSUMÉ. – Plusieurs spécimens de *Cirrimaxilla formosa* (Muraenidae) ont été trouvés dans les estomacs de serpents de mer *Laticauda laticauda* et *Laticauda saintgironsi* capturés en Nouvelle-Calédonie dans le cadre d'une étude écologique sur ces serpents. Ces spécimens représentent le premier signalement de *C. formosa* en Nouvelle-Calédonie. Cette murène n'était jusqu'à présent connue que par son holotype récolté dans le sud de Taiwan.

KEYWORDS: Muraenidae, *Cirrimaxilla formosa*, New Caledonia, First record

1 INTRODUCTION

Sea kraits (Elapidae, Hydrophiinae) are large (up to 1.5 TL) venomous sea snakes that forage in the ocean mostly on anguilliform fishes (Pernetta, 1977; Shetty, 2000; Shetty and Shine 2002b; Reed *et al*., 2002; Ineich and Laboute, 2002). Sea snakes community represents an efficient sampling tool for anguilliform fishes such as the eels (moray, conger and snake eels) that live in holes and crevices of the reef (Reed *et al*. 2002, Ineich *et al*. 2007). Indeed, a previous study had recorded about 44 species of morays, congers and snake eels found in the stomachs of sea snakes (Ineich *et al*., 2007).

In the frame of an ecological study on the New Caledonian sea snakes (FB thesis), the stomach contents of two species of sea snakes, *Laticauda laticaudata* (tricot rayé bleu, brown-lipped sea krait) and *L. saintgironsi* (tricot rayé jaune, yellow-lipped sea krait) were analysed in order to determine their diet.

Among the moray eels recorded, 16 specimens of *Cirrimaxilla formosa* Chen and Shao, 1995, were found in the stomachs of the two species of sea snakes. These specimens represent the first record of *C. formosa* from New Caledonia. This moray was recently described from a single specimen found in a tidal pool in Nanwan, southern Taiwan; this holotype is preserved in the collection of the Museum of the Institute of Zoology, Academia Sinica (n° ASIZP.056729, 166 mm TL).

2 MATERIAL AND METHODS

The two species of sea snakes *L. laticaud*ata and *L. saintgironsi* were collected mainly on the beaches of islets Amédée and Signal, situated in the southern lagoon of New Caledonia, during several surveys carried out between January 2005 and February 2006. The sea snakes were captured by hand, measured, tagged and released. Stomach contents were obtained through gentle palpation of the snakes to force them to recurgitate. Each prey item was weighted, measured and preserved

for later identification. Five *L. saintgironsi* and 11 *L. laticaudata* had specimens of *C. formosa* in their stomachs; the capture data are given in Table 1.

TABLE 1 – *Capture data related to the specimens of* Cirrimaxilla formosa *found in the stomachs of the two species of sea snakes* Laticauda laticaudata *(LL) and* L. saingironsi *(LS).*

N° moray	Sea snake	Locality	Date	Swallowed by	Trunk Length mm	Tail Length mm	Total Length mm
29-1	LS - 685	Signal	24.01.2005		160	120	280
29-2	LS - 685	Signal	24.01.2005	tail			
137	LS - 818	Larégnère	11.02.2005	tail			
426	LS - 1187	Amédée	7.04 2005	head			
504	LS - 1288	Amédée	8.05.2005	head	190	135	325
160-1	LL - 843	Amédée	16.02.2005	head	160	100	260
160-2	LL - 843	Amédée	16.02.2005	head			
227	LL - 914	Amédée	17.02.2005	tail			
306	LL - 1040	Mba	12.03.2005	head			
513	LL - 1114	Amédée	9.05.2005	tail			
581-1	LL - 1188	Amédée	13.11.2005	head			
581-2	LL - 1188	Amédée	13.11.2005	head	140	100	240
587	LL - 1212	Amédée	14.11.2005	tail	265	155	420
591	LL - 921	Amédée	15.11.2005	head	145	100	245
818	LL - 21	Signal	14.02.2006	tail			
819	LL - 1523	Signal	14.02.2006	tail			

A specimen in good shape (Fig. 1) was deposited in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN 2007-0126).

FIG. 1 – *Picture of the specimen MNHN 2007-0126 of* Cirrimaxilla formosa, *320 mm TL, found in the stomach of sea snake* Laticauda laticaudata, *captured in Amédée islet, New Caledonia. The digested posterior part of the body shows that this specimen was swallowed by the tail.*

3 Results and discussion

The snakes swallow their prey either by the head or by the tail, and because of their length, the morays are digested gradually as they enter into the stomach. Depending on the digestion rate, prey may be intact or have either their anterior or posterior part digested. Thus, it was possible to identify the species in using the original description of *C. formosa,* which is the only reference available on this species (Chen and Shao, 1995).

The diagnostic characteristics of *C. formosa* were shared by the New Caledonian specimens: dorsal and anal fins restricted to tip of tail (subfamily Uropterygiinae); tail shorter than trunk; lower jaw protruding; posterior nostril oval with raised, petal-shaped rim, hooked fang-like teeth, margin of both jaws with many beard-like cirri (genus *Cirrimaxilla*); along with the distinctive colour pattern of the species consisting in a conspicuous dark brown network of anastomosed stripes on a tawny background.

Among the 16 specimens of *C. formosa* found in the stomachs, 6 were in good shape enough to measure or estimate their total length (Table 1) varying from 240 mm to 420 mm TL. These are adult specimens since the Taiwanese holotype was a gravid female of 160 mm LT.

These records extend greatly the distribution of *C. formosa*, which is so far only known from southern Taiwan. Its geographical range might even be larger as without the "help" of the sea snakes, the species would not have been recorded from New Caledonia. The type of *C. formosa* was found in a tidal pool in southern Taiwan, but in New Caledonia, this species must live hidden in deep reef holes and inaccessible to any fishing gear. Logging studies (still under way - unpublished data), have shown that the sea snakes are likely to leave the reef to dive on the external slope down to 80 m depth. Thus, these specimens of *C. formosa* may have been captured by snakes during deep dives. Alternatively, this species may present a secretive ecology, being undetectable to classical fish sampling (Ineich *et al.* , 2007). In Taiwan, the sea snakes do not feed on moray eels; hatchling snakes feed on Mugiloididae, subadult and mature snakes on Emmelichthyidae, Acanthuridae and Pomancentridae (Su *et al.*, 2005), showing a wide range of adaptation of their feeding habits.

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Are sea snakes pertinent bio-indicators for coral reefs? A comparison between species and sites

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Manuscript in preparation

1 INTRODUCTION

Given the rate of biodiversity loss and because there is no geographic area spared by global changes, it is crucial to gather rapidly information on representative species to evaluate the conservation status of a wide variety of ecosystems (Vitousek et al. 1997). Unfortunately most animal species are highly cryptic, inaccessible and impossible to sample in significant numbers. To circumvent such difficulties, some species can be used as natural gauges or bio-indicators (McGeogh 1998). In terms of cost/efficiency ratio, useful indicators should combine a number of characteristics (Noss 1990; Pearson and Cassola 1992; Niemelä 2000). Notably, they should be widely distributed and their trophic ecology should be described. Such prerequisites are essential to allow inter-site comparisons and to assess the reasons underlying the observed trends, especially when the erosion of biodiversity is rapid. Bio-Indicators should exhibit a high degree of ecological specialisation to probe accurately relevant (and ideally uncontroversial) functional aspects of the ecosystems. To monitor of a specialised predator enables to survey indirectly but precisely the underlying trophic levels represented by its main preys (Ineich et al. 2007). In addition, specialised species are far more vulnerable compared to generalists, and therefore require particular attention. Finally, to be useful at a large scale, bio-indicators should be logistically easy to survey. Facing such a range of desired characteristics, it is difficult to find the appropriate bio-indicator for all the threatened major ecosystems.

Coral reefs provide one of the typical examples of extremely rich ecosystems that are suffering deep worldwide ecological crisis (Rogers 1990; Hughes 1994; Guinotte et al. 2003; Pandolfi et al. 2003; Sheppard 2003; Bellwood et al. 2004). Coral reefs also cumulate the problem of an insufficient knowledge of the ecological role and diversity of much of the species that remain sheltered in the coral matrix. For instance, important communities of coral reef predators such as a wide variety of anguilliform fish (henceforth named eels for simplicity) remain poorly known (Kulbicki 1997; Abrams et al. 1983). An examinaton of FishBase (Froese & Pauly

2006) reveals that most of the eel species are known from isolated specimens associated with a virtually total lack of ecological information. Recently, it has been suggested that a group of sea snakes specialized on eels, the sea kraits (*Laticauda* spp.), could be useful bio-indicators to survey the biodiversity of the anguilliform fish communities in coral reef ecosystems (Reed et al. 2002, Ineich et al. 2007, Seret et al. 2007). Indeed, analysis of sea kraits stomach contents revealed unexpected densities and species richness of eels in the several coral reef areas sampled (Vanuatu: Reed et al. 2002; New Caledonia: Ineich et al. 2007, Seret et al. 2007). For instance, in New Caledonia, eels sampling through sea kraits revealed 15 new fish species for the area and indicated that eel densities were underestimated by several orders of magnitude (Ineich et al. 2007).

As possible bio-indicators to monitor important, albeit neglected, components of the biodiversity of the coral reef animal communities, sea kraits fulfil the requirements listed above. First, they exhibit an enormous distribution range, broadly from the bay of Bengal to the Tonga archipelago and from Japan to New-Caledonia (Heatwole 1999). Second, their foraging ecology is now well documented in various places (Fidji, Vanuatu: Reed et al. 2002, Shetty & Shine 2002d, Shine et al. 2002b; New Caledonia: Brischoux & Bonnet 2007, Brischoux et al. 2007a, b; Ryukyu archipelago: Su et al. 2005). Sea kraits are highly specialised on more than 50 species of eels, that are themselves predators. Because sea kraits swallow preys whole and because it is easy to force them to regurgitate, a large proportion of the preys collected are intact or poorly digested (Brischoux and Bonnet 2007, Brischoux et al. 2007a, b) facilitating the identification and counting of the preys; and thus enabling in turn to study the eels themselves (including their own preys). Therefore, sea kraits can be used to assess different trophic levels in a straightforward way. Third, sea kraits occur in very high densities and are extremely docile during handling, rendering any survey cost-effective (Brischoux and Bonnet 2007). Finally, their marked philopatry toward their home islet offers a powerful and simple way for

comparisons between different sites within and among broad geographic areas (Shetty & Shine 2002).

Overall, sea kraits display a large range of advantages to assess the diversity and the abundance of many species of eels, and therefore to probe accurately otherwise hidden and inaccessible components of the coral reef communities. Such statement remains partly hypothetical however. Indeed, to appreciate the pertinence of sea kraits for bio-indicators, crucial information is still lacking. For instance, we do not know if each population of sea kraits exhibits a peculiar diet, or alternatively if geographic variations are minor. Such knowledge is central to set up and interpret long term monitoring. Using two species of sea kraits (*L. laticaudata* and *L. saintgironsi*) and five different sites in the Neo Caledonian lagoon, the aim of this study was to determine what are the sample sizes required to utilise sea kraits as biodiversity indicators of eels with satisfactory confidence, and to explore possible small spatial scale variations in eels assemblages.

2 MATERIAL AND METHODS

2.1 Study species and sites

Two species of sea kraits (Elapidae, Hydrophiinae) occur in New Caledonia: *Laticauda saintgironsi* (Cogger & Heatwole 2006) and *L. laticaudata* (Ineich & Laboute 2002, Saint Girons 1964). We surveyed the sea krait populations of 9 different islets in the southwest lagoon of New Caledonia (fig 1, Brischoux & Bonnet 2007). However, fore the purpose of the current study we selected five sites that provide sufficient data on snake diet to ensure more balanced samples: from North to South, Ténia, Mba, Signal, Larégnère and Amédée (figure 1). Although *L. saintgironsi* was present in all the sites surveyed, large resident populations of *L. laticaudata* occurred in solely three of them (Mba, Signal and Amédée). Snakes were collected by hand, measured (snout vent length-SVL, ±1cm), weighed (±1g) and individually marked by scale clipping (Brischoux & Bonnet 2007).

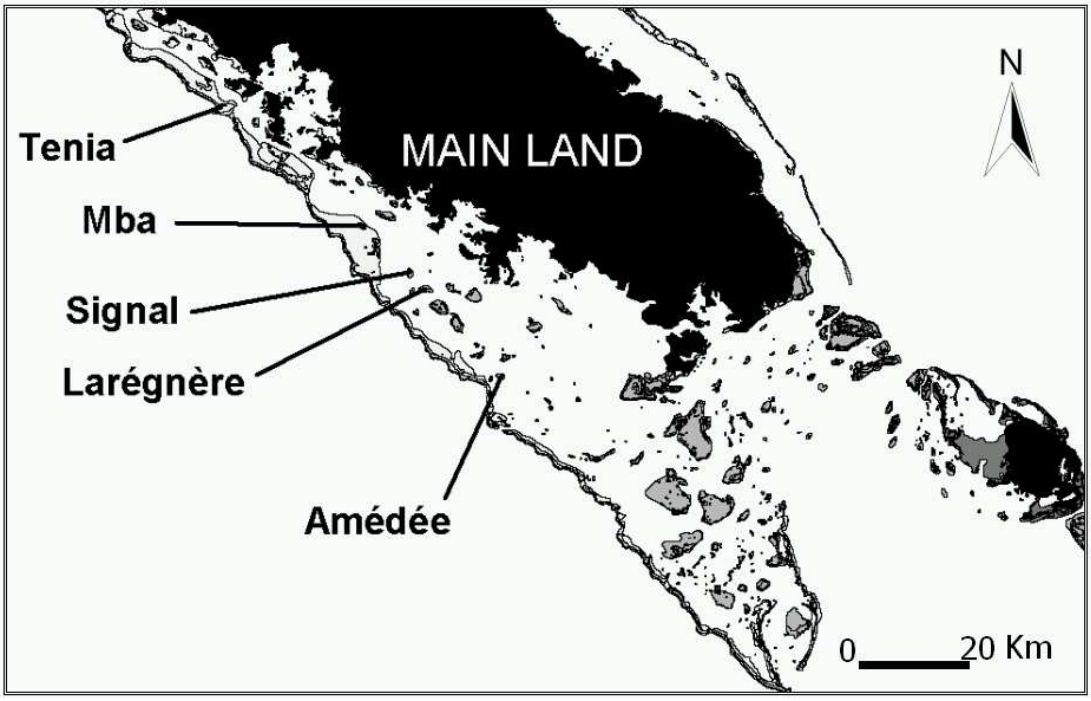

FIG. 1 - *Map of the south-western lagoon of New Caledonia. Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by light grey areas.*

The abdomen of each snake was carefully palpated to check for the presence of prey in the stomach. As sea-kraits feed essentially on non-spiny fish, it was easy to force them to regurgitate their preys (Brischoux and Bonnet 2007). Each sea krait species exhibits a peculiar diet with a low overlapping (13%) between them, and they do not forage in the same area: essentially hard bottoms for *L. saintgironsi* versus soft and hard bottoms for *L. laticaudata* (Brischoux et al. 2007b). Therefore, the two species provide a separate opportunity to investigate their ability to gauge the eel communities and to perform comparisons between sites.

We collected, identified, measured and preserved 1,077 regurgitated prey items (see Brischoux et al. 2007a for details). Data on prey habitat were gathered from FishBase (Froese & Pauly 2006). Habitat requirements were obtained for 29 out of

the 49 eel species consumed by the sea-kraits (this lack of basic ecological information for roughly 50% of the preys illustrates the insufficiency of knowledge of these systems). For simplicity, we categorised habitats into three broad types: hard bottom, soft bottom and hard plus soft bottom (see Brischoux et al. 2007b).

2.2 Analyses

Classically, to compare species diversity between sites, a minimal sample size is required. This sample size is obtained using saturation curves (Chao estimator, Colwell, 2005). In our case, minimal required sample size was more than 50 (unpublished data). However for some sites, the sample size of regurgitated "eels" was lower (Mba for *L. laticaudata*, Mba and Ténia for *L. saintgironsi*). In order to keep those sites in our analyses, we used alternative techniques that allow to take into account such disparity in sample size between sites. Accordingly, we used two complementary approaches: (i) analyses of similarity (ANOSIM, Clark 1993) that compares the differences in assemblage compositions, and (ii) species richness estimates (Shannon diversity index, Magurran 1988; and standard rarefaction technique, Koellner et al. 2004). Further details are provided below.

Analyses of similarity (ANOSIM)

ANOSIM is a non-parametric test designed to evaluate spatial differences and temporal changes in the assemblages of organisms (Clark 1993, Chapman & Underwood 1999). ANOSIM procedures are based on the comparisons of intra and inter group distances calculated as average ranked values (often the Bray-Curtis measures of dissimilarity) in abundances and types of organisms among replicates between samples. The output statistic provides R-values ranking between -1 and 1, and a P value to help in the decision making: two sampled units are considered as similar when R is equal to 0 and as totally different when R is equal to 1 (or –1,

although negative value pose interpretation difficulties, see Chapman & Underwood 1999).

Species richness

As the sampling effort was unevenly distributed, we performed two different approaches to estimate the species richness.

First, we calculated Shannon diversity indexes to compare species richness of sea krait diets between islets. However, because Shannon index is very sensitive to sample size bias (Magurran 1988), we relied on 1,000 random sub-samplings for each site to compare the distributions of Shannon diversity indexes between the sites. For that, we standardised the sampling method between the islets. The sample size was set up at 38 randomly sorted preys for *L. saintgironsi* and 24 preys for *L. laticaudata*; these values correspond to the minimal common sample size among all sites. Then we performed another random sub-sampling set up at 90% to generate a distribution of Shannon indexes.

Second, we used standard rarefaction technique widely used to compare the number of species in a collection of samples with uneven sample sizes (Koellner et al. 2004). Rarefaction is a procedure for analyzing the number of species (species richness) among collections, when all collections are scaled down to the same number of individuals. The number of species can be expected from a random sample of individuals, drawn without replacement from individuals distributed among species. We calculated the estimated number of species for each study site based on the smallest sample size (depending on the snake species).

3 Results

3.1 Analyses of similarity and diversity indexes

ANOSIM and diversity indexes led to similar trends, thereby simplifying the interpretation of the results that combine respectively statistical and graphical approaches (Table 1, figure 2). All the indexes of similarity were small (R<0.14), the curves between sample size and the expected species number followed similar trends, and the Shannon indexes remained within relatively narrow ranges. Beside these broad trends, significant differences have been detected between the sites.

TABLE 1 - *ANOSIM tests for each of the pair-wise comparisons of the diet of sea kraits between islets. 10 pair-wise comparisons were performed for of* L. saintgironsi *(LS, 5 islets) and 3 pair-wise comparisons for* L. laticaudata *(LL, 3 islets). For each comparison, the values given are the R-statistic, and its p-value in parentheses. Values given in bold are statistically significant. NP indicates comparisons that were not performed (see materials and methods).*

Species	Site	Amédée	Larégnère	Mba	Signal
LS	Larégnère	0.025 (0.097)			
	Mba	**0.138 (0.001)**	**0.050 (0.025)**		
	Signal	0.003 (0.207)	0.011 (0.293)	**0.099 (0.009)**	
	Ténia	-0.017 (0.643)	-0.033 (0.894)	**0.055 (0.004)**	-0.029 (0.759)
LL	Mba	**0.108 (0.005)**	NP		
	Signal	**0.046 (0.001)**	NP	0.019 (0.221)	

For *L. saintgironsi*, one islet, "Mba" provided a greater diversity of the anguilliform fish community that significantly differ from the four other sites. All the other sites were relatively similar, although one indicator, the expected species number, suggested that the diversity of the preys found in the stomach of the snakes was lower in Amédée Island (figure 2a).

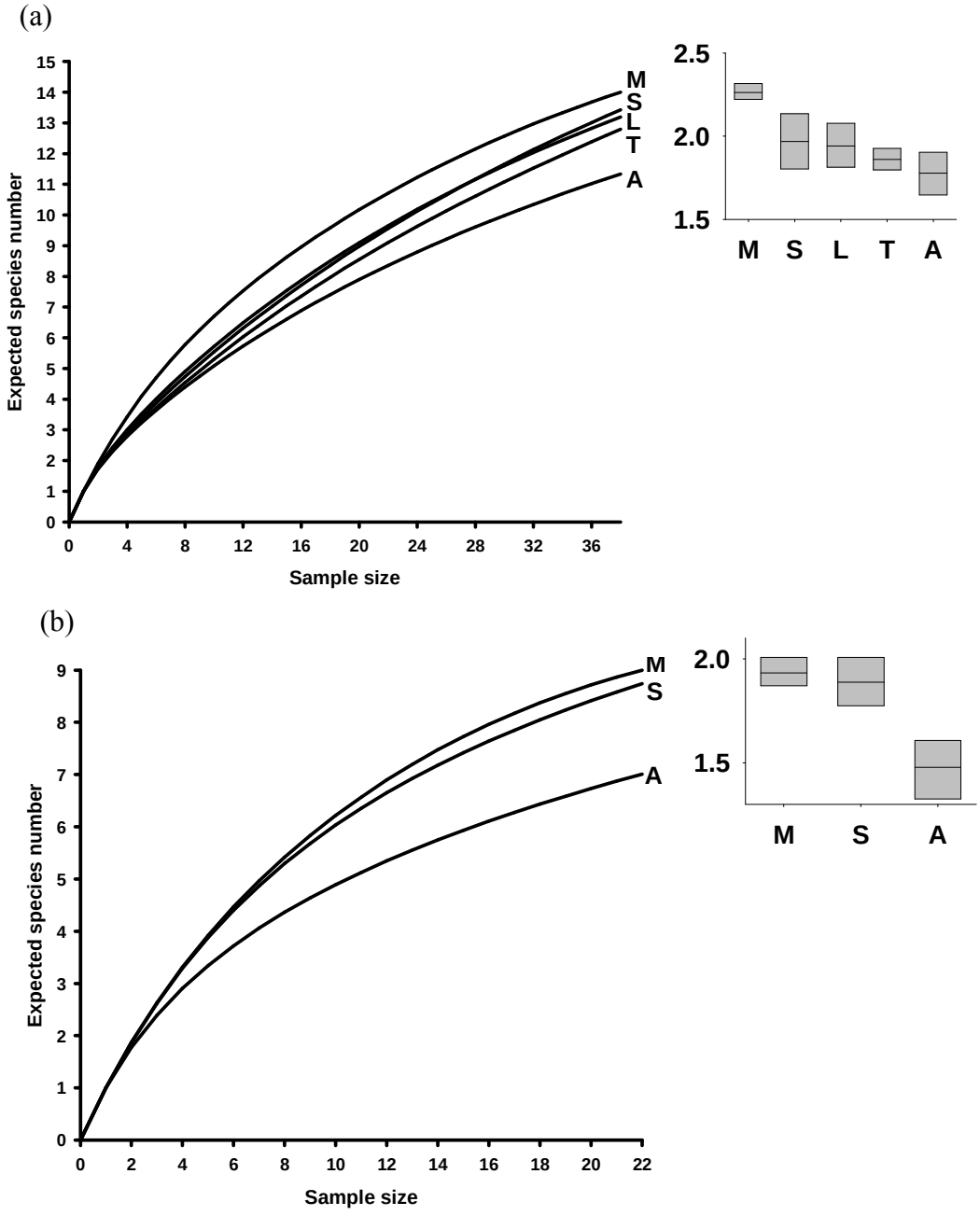

FIG. 2 - *Expected species number of eels (major figures) for the different study sites for* L. saintgironsi *(a) and* L. laticaudata *(b). Minor figures indicate the Shannon diversity index distribution calculated through bootstraps. M, S, L T, and A stand respectively for Mba, Signal, Larégnère, Ténia and Amédée.*

For *L. laticaudata*, the community of preys as revealed by snake sampling around Amédée Island was significantly poorer compared to Signal or Mba Islands (Table 1, figure 2b). Interestingly, although the two species of snakes exhibit peculiar dietary and foraging habits, the analyses of their stomach contents provided biodiversity indexes that ranked the sites exactly in the same order (i.e. from the more to the less diverse: Mba > Signal ≥ Larégnère ≥ Ténia > Amédée for *L. saintgironsi* and Mba ≥ Signal>Amédée for *L. laticaudata*; figure 2).

3.2 Prey habitat

The analyses of the prey habitat information collected on FishBase (Froese & Pauly 2006) revealed that *L. saintgironsi* take similar proportions of prey from hard-bottoms versus hard-soft-bottoms in all the five sites, and that most of the preys (95%) are typical from hard bottom substrates (Figure 3a; χ^2=2.71, df=4, P=0.60). By contrast, such proportion differed markedly between the three sites for *L. laticaudata*; for instance most of the preys are typical from soft bottoms around Signal Island, but typical from hard bottoms around Amédée Island (Figure 3b; χ^2=176.08, df=4, P<0.001).

4 Discussion

Using two species of sea krait as separate entities, our results provided consistent estimates between our study sites. The relationship between sample size and the richness of anguiliform fish followed similar curves; and the similarity indexes remained always close to zero. Would the sampling method we employed have been imprecise, the possibility to find regular trends would have been very unlikely. Therefore, the similarity between the different estimates employed (ANOSIM, Shannon index…), indicates that the specific assemblages of the fish captured by the sea kraits was sampled with a satisfactory accuracy.

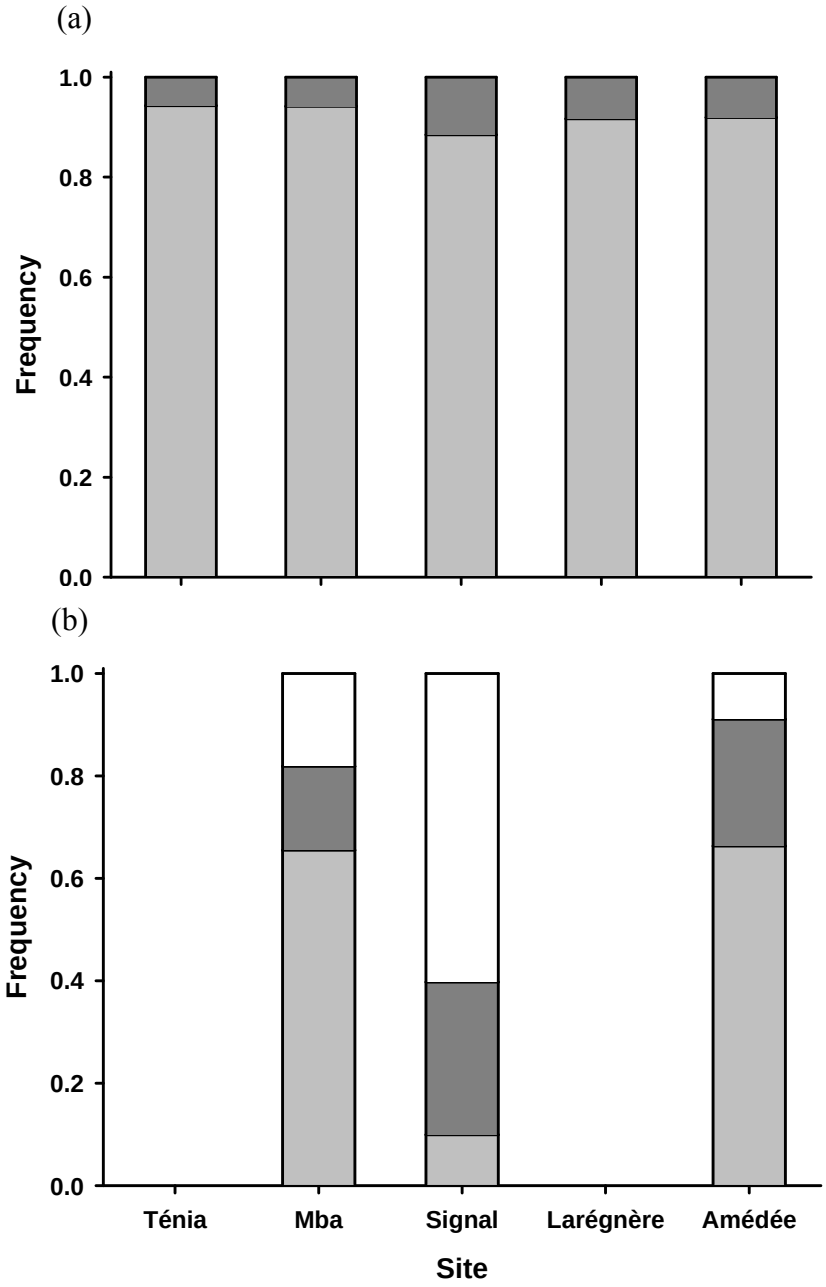

FIG. 3 - *Proportion of prey living in the three habitat types (light grey: hard bottoms, dark grey: soft bottoms, white: hard and soft bottoms) for each study sites. Upper figure for* L. saintgironsi *(a) and lower figure for* L. laticaudata *(b).*

Such estimates permitted to minimize the bias due to unevenly distributed sample sizes. A combination of factors explains the regularity in the results we obtained in different sites: sea kraits are highly specialised on anguiliform fish, as gape-limited predators they select precise prey sizes, they forage continuously around their home islet and are limited to a 17 km radius around, and their hunting technique relies on the systematic exploration of the cavities in the substrate. Overall, the trophic links between the sea kraits and their preys appears to be very tight, and such tightness automatically leads to the precision in the associated estimates.

Although we do not have access to the population dynamics of the eels consumed by the snakes, straightforward albeit indirect information can be extracted from the sea kraits monitoring. In this perspective, snakes present a number of advantages. As ectothermic vertebrates they exhibit a low metabolic rate; the assimilation rate of the food that can be converted into snake's tissues is particularly high (Pough 1980; Bonnet et al. 1998). Consequently, variations in food intake translate into parallel and long lasting variations of snake's body mass; and such effects are easily measured in the field. By comparison, in classical bio-indicators such as sea birds, most of the resources consumed are used to sustain a very high metabolic rate. In addition, snakes exhibit indeterminate growth pattern, strong variations in body condition, in reproductive frequency and reproductive output (fecundity, offspring size); and all these parameters are strongly influenced by food intake (Bonnet et al. 2001, 2002b). In other words, the comparisons of a set of these characteristics such as mean snake body size, body condition, etc. would provide a way to assess the relative abundance of the eels between sites and years.

Our results also suggest subtle but significant differences between the islets.

For *L. saintgironsi*, both ANOSIM and diversity indexes indicated that the sea krait population belonging to Mba feed on different and more diverse prey species. For instance, the proportion of the main prey, *Gymnothorax chilospilus*, was lower compared to other sites (25% in Mba *versus* 50% for all the other sites). Other eel

species were more represented in the stomach of the Mba snakes: for example *G. fimbriatus* (18% *versus* 7%), *G. margaritophorus* (13% *versus* 5%) and *G. undulatus* (5% *versus* 1.5%). Interestingly, the surroundings of Mba belong to a particular structure of the lagoon: a shallow lagoon plateau that is connected to the barrier reef (Andrefouët et al. 2004; Fig 1). For *L. laticaudata*, the foraging habitat was more variable (Figure 3b) between the islets. The higher proportion of eel species that live in hard bottoms of Mba and Amédée islets was presumably due to the predominance of hard substrates around the shallow lagoon plateau for Mba and the coral bottoms from the barrier reef for Amédée compared to Signal Island (Figure 1). ANOSIM and diversity indexes indicated that Amédée was less diverse and dissimilar from Signal and Mba. Interestingly, such results converge with the differences observed with the diet of *L. saintgironsi*: sites near the barrier reef (Ténia and Amédée for *L. saintgironsi*; Amédée solely for *L. laticaudata*) seem to shelter less diverse eels assemblages. We thus hypothesis that the structure of the lagoon sea floor affects diversity and abundance of eel species.

In terms of bio-indication to gauge anguiliform fish associated with coral reef ecosystems, *L. saintgironsi* seems to be the best candidate. Compared to *L. laticaudata*, this species is more ubiquitous and easier to sample, the proportion of foraging habitats is more repeatable, which simplify analyses. Nonetheless, the ecological peculiarities of *L. laticaudata* mean that this species can provide complementary information. Overall, the diversity of sea krait species, their large geographic range and the variation in diet between sites and species make sea kraits a powerful bioindicator perform geographic comparison of the eels community at small (e.g. south west neo-caledonian lagoon) and large (e.g. Indo-Pacific coral reefs) spatial scales, but also give access to an important, albeit unknown, part of the anguilliform fish ecology in coral reef areas.

Résumé du Chapitre

Ce chapitre est de loin le plus long et le plus dense de ce manuscrit. Pourtant, *a priori*, c'est bien sur cette partie de l'écologie des tricots rayés que l'on possédait le moins de données et que ces données étaient le plus difficile à collecter. Il est en effet beaucoup plus facile d'observer ces animaux à terre qu'en mer, notamment grâce à leurs densités élevées et à leur comportement docile mais aussi parce qu'il n'est pas nécessaire d'avoir un équipement lourd (qui n'existe malheureusement pas encore !) qui permettrait de suivre des animaux sous l'eau pendant plusieurs jours.

L'existence d'enregistreurs automatiques de données a, tout d'abord, permis de lever le voile sur leur activité en mer. Ces animaux ont une activité de nage et de plongée continue sur toute la durée de leurs voyages en mer, même si ceux-ci dépassent allègrement les dix jours. Outre la mise en évidence de leur durée d'activité très inhabituelle, de telles données ont permis d'explorer les paramètres classiquement étudiés chez les animaux plongeurs. Les serpents marins font encore exception aux règles classiques qui régissent le comportement de plongée chez d'autres vertébrés marins à respiration aérienne (voire aussi l'annexe I). Malheureusement, le faible nombre d'enregistreurs déployés n'a pas permis de s'appuyer sur une comparaison des deux espèces pour ces paramètres de plongée (durée des voyages, profondeurs moyennes ou maximales,…).

En passant par l'étude détaillée de leur régime alimentaire, il été possible de dévoiler des pans entier de leur écologie alimentaire sous-marine. En effet, même si les poissons anguilliformes sont, de loin, extrêmement peu connus, le peu de données existantes nous ont néanmoins été très précieuses. L'obtention des proies grâce à la régurgitation forcée nous a permis d'avoir accès à des poissons qui se situent dans un gradient de degrés de digestion. Une telle situation a été extrêmement avantageuse pour mettre en place une méthode qui permette de reconstruire la taille et la masse originelle d'une proie en partie digérée. Si cette méthode est indispensable pour étudier les relations taille de la proie-taille du

prédateur, par exemple, elle a également été cruciale pour reconstruire la durée des voyages retour, du lieu de pêche à l'îlot de résidence. Combinées à des mesures de vitesse de nage, ces mesures de temps de voyage retour ont permis de déterminer à quelle distance d'un îlot les tricots rayés vont s'alimenter.

En outre, à travers les habitats utilisés par les poissons anguilliformes, nous avons pu mettre en évidence que les deux espèces de tricots rayés de Nouvelle-Calédonie ne s'alimentent pas dans les mêmes zones, le tricot rayé bleu favorisant les fonds meubles alors que le tricot rayé jaune explore la matrice corallienne. De telles divergences ne sont pas anodines et agissent de manière forte sur les écologies de ces deux espèces de serpents. En effet, les habitats des proies imposent au serpent de modifier éventuellement son régime alimentaire au cours de sa vie.

Enfin, l'examen et l'identification des proies des tricots rayés a permis de mettre en exergue leur rôle de bio-indicateurs. Notamment, grâce à ces prédateurs, nous avons mis en évidence une diversité et une densité de poissons anguilliformes bien supérieure à ce qui avait été estimé jusqu'à présent (pour une analyse plus détaillée, voir aussi l'annexe II).

La vie sous-marine des tricots rayés ne correspond qu'à la moitié de leur temps. Ces animaux passent l'autre moitié de leur vie à terre. N'évoquer que leur vie en mer est évidemment trop limité pour avoir une vision d'ensemble de leur écologie. Les différences entre ces animaux sont-elles aussi marquées à terre qu'elles le sont en mer ?

Chapitre III

ECOLOGIE TERRESTRE DES TRICOTS RAYÉS

RETOUR À TERRE

Precise site fidelity in sea kraits: implications for conservation

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Manuscript in preparation

1 INTRODUCTION

Coral reefs, well known biodiversity hot spots (Roberts et al. 2002), are going through a deep crisis that is worsening over time (Rogers 1990; Hughes 1994; Guinotte et al. 2003; Pandolfi et al. 2003; Sheppard 2003; Bellwood et al. 2004). The causes of such calamity are diverse: global warming, over-fishing and marine pollution are among the main factors affecting coral reefs (Walker & Ormond 1982; Linden 1999; Hughes et al. 2003; Riegl 2003). Considerable effort has been devoted to understand how these complex ecosystems function and beside fundamental contributions, such knowledge is crucial to set up relevant conservation issues.

Predation may greatly influences the coral reef ecosystems, by enhancing the stability (resilience) of the whole community (Carpenter et al. 1985; McCann et al. 1998; Finke & Denno 2004). However, detailed studies on predation in reef ecosystems are lacking because of the difficulty to set up such studies (Hixon 1991, Caley 1993). Recent studies have highlighted the ecological role of a community of predator neglected so far: sea snakes (Reed et al. 2002, Ineich et al. 2007) which might be considered as indicator species for reef health (Alcala 2004). Among sea snakes, sea kraits have been shown to play a key role in coral reefs ecosystems as they feed on remarkable quantities of anguilliform fishes (mostly moray eels), top-predators themselves (Ineich et al. 2007, FB, XB unpublish data).

These particular marine snakes might be very sensitive to perturbations because of their amphibious lifestyle. They forage at sea but come back on land to digest, mate, lay their eggs and slough their skin (Heatwole 1999, Ineich & Laboute 2002, Brischoux & Bonnet 2007) and are philopatric to their home islet (Shetty & Shine 2002a).

As a consequence, we can expect that sea kraits would be doubly vulnerable, to disturbances on marine ecosystem *per se* but also to habitat modification on their home islets. Although their foraging ranges (and thus the spatial scale over which at sea disturbances can affect a sea krait population) have been recently assessed (Brischoux et al. 2007b), the degree of their philopatry is not known yet. The aim of

this study was to assess the degree of the sea kraits philopatry to their home islet (i.e. a global philopatry to the whole home islet versus a specific attraction to a precise area of their home islet).

2 MATERIAL AND METHODS

2.1 Study species

Two species of sea-kraits occur in New Caledonia: *Laticauda saintgironsi* (endemic to the area, Cogger & Heatwole 2006) and *L. laticaudata* (Ineich & Laboute 2002, Saint Girons 1964). We surveyed sea kraits populations on 9 islets, situated in the south west lagoon of New Caledonia (from the north to the south: Tenia, Mba, Signal, Larégnère, Porc-Epic, Amédée, Nouaré, Bayonnaise and Brosse; Brischoux & Bonnet 2007). For each individual, the species and the sex were recorded. Snakes were measured (snout vent length-SVL, ±1cm), weighted (±1g) and individually marked by scale clipping (Brischoux & Bonnet 2007).

2.2 Capture areas

On Signal islet a 6-ha, flat and rectangular islet (22°17′45 S; 166°17′34 E), we patrolled a 450-m section (west beach) of the shore comprising flat beach rocks (80%) and small sandy beaches (20%). This study site was divided in 45 areas of 10m long and for each snakes, we recorded the area of capture. To test if the successive captures of a given individual occurred mainly in a particular area (individual fidelity) or occurred randomly (no fidelity to an area), the mean observed distance between each successive capture of a given individual was compared to the mean distances simulated according to the null hypothesis (no area fidelity). To obtain these simulated distances for each individual, *n* areas (corresponding to the total number *n* of capture events for this individual) were randomly chosen (resampling

with replacement) from the total pool of capture events for the considered species. This design allowed taking into account the preference for particular area of each species. The mean simulated distances between successive captures for each individual was computed and compared to its observed mean, each individual contributed with the same weight in the analyses.

We also performed a translocation experiment at a small spatial scale. In 2004, more than 270 snakes (179 *L. laticaudata* and 98 *L. saintgironsi*) captured on the west shore of Signal Islet were released on the east shore.

3 Results

3.1 Translocations

We recaptured 47% of the translocated snakes for *L. saintgironsi* and 76% for *L. laticaudata*. Such interspecific differences accord well with the differences in recapture rates (52% in *L. saintgironsi*, χ^2=0.02, df=1, p=0.9 and 77% in *L. laticaudata*, χ^2=0.02, df=1, p=0.9).

For both species, 100% of the recaptured translocated snakes came back on the shore of capture (elapsed time between captures 1 day to 3 years).

3.2 Capture areas

We gathered data on capture areas for 405 *L. laticaudata* (mean 3.15 capture areas per individuals, max=11) and 175 *L. saintgironsi* (mean 2.47 capture areas per individuals, max=6). Observed means were significantly smaller than random means (paired t-test, t=-10.45, df=403, p<0.0001, for *L. laticaudata* and t=-4.09, df=173, p<0.0001, for *L. saintgironsi*, Fig. 1). Restricting analyses to individuals with more than 2 observations led to similar results.

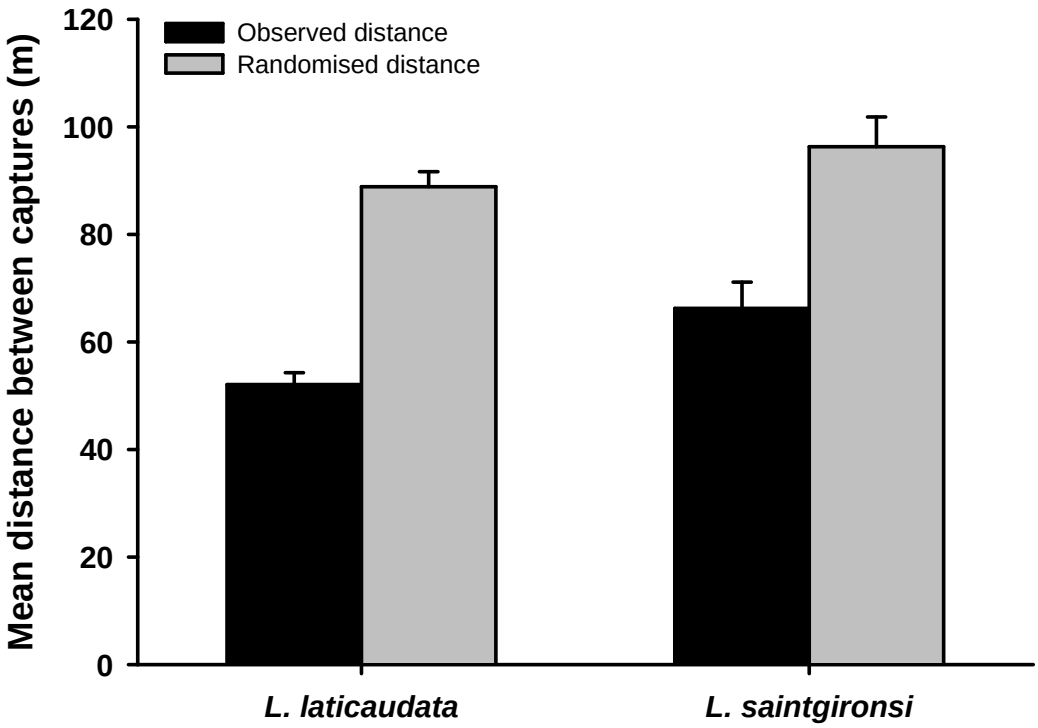

FIG. 1 – *Mean distance between capture for* L. laticaudata *and* L. saintgironsi. *Randomised distance were obtained through resampling with replacement.*

4 Discussion

Philopatry and homing behaviour have been shown in sea kraits from Fiji (*L. colubrina*, Shetty and Shine 2002a) at a broader spatial scale (i.e. the whole islet). In this study, we showed that sea kraits display an extremely precise philopatry toward an home islet: over a 450 m long beach, each individual tended to be captured and re-captured within a 60 m area. Our results showed that sea kraits do not only come back "home" after a foraging trip but select a very precise area of their home islet. Such fidelity suggests that sea kraits know precisely their terrestrial environment and the shelters they use when on land (large beach rocks, sea birds

burrows, unpublished data). Such knowledge may reduce significantly the transit time between the sea and the terrestrial shelter; which might be important to reduce exposure to predators (sea eagles for instance), and might allow the snakes to rapidly reach the thermal optimum needed to perform most of their terrestrial activity (digestion, sloughing and reproduction, Brischoux & Bonnet 2007) by evading overheating or overcooling.

Several observations of *L. saintgironsi* coming back to land suggest that this species could locate shore areas by sight: snakes were often displaying a periscope behaviour while swimming in parallel to the shore (pers. obs.). On the other hand, although *L. laticaudata* were often seen swimming in parallel to the shore, this species is nocturnal and probably rely on other clues to locate shore areas (e.g. olfactory clues).

Considering conservation issues, such precise philopatry implies particular habitat management. The terrestrial habitat of sea kraits might be affected by human activities (e.g. resort activities) that would affect the availability of natural shelters and might lead to extinction of local populations. Several type of habitat modifications (resort construction and islet inhabiting) already affected and even eliminated sea krait populations in New-Caledonia (Brischoux and Bonnet 2007). In turn, such disturbance to sea krait populations would affect the predation pressure on anguilliform fish (top predators themselves) over a great spatial scale (hundreds of km², Brischoux et al. 2007b).

As the reverse reasoning is also true (at sea disturbances can influence predators based at islands many kilometres distant), such issue clearly revealed that both habitats (islets but also the whole lagoon) have to be considered in management planning. In New-Caledonia, marine reserves (mainly centred on islets) are usually a few tens of km² (mean 16.3 km², range: 0.001-172 km², N=17) and we suggest that the spatial scales of these marine reserves need to be reconsidered to provide effective protection for these indicator species for reef health (Alcala 2004).

LA SELECTION DE L'HABITAT

Beach-rocks are keystone habitats for sea kraits

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Abstract. Most species of sea kraits (Laticaudid sea snakes) face major threats worldwide. Firstly, sea kraits are tightly dependent on coral reefs to find their food (anguiliform fish), but the preservation of these marine ecosystems is compromised in many areas. Secondly, massive hunting for skin and meat trade causing local population extinctions has been documented in different places. Third, sea kraits also depend on terrestrial habitats (e.g. refuges to digest their preys), but the shore of small islets is also coveted for tourism and hence under strong anthropogenic pressure. In this study, we focused on the terrestrial habitat used by two sympatric species of sea kraits: *Laticauda laticaudata* (blue sea krait) and *L. saintgironsi* (yellow sea krait). The yellow sea kraits are able to climb steep cliffs, to travel relatively long distances on land, and consequently to use a great variety of terrestrial shelters. By contrast, blue sea kraits are poor climbers and are constrained to remain very close to the shore. Very peculiar types of beach-rocks are essential for the blue sea kraits: between foraging trips, these snakes shelter under beach-rocks, easily accessible from the sea, regularly submerged at high tide but by no more than a maximum of 30cm of water to allow aerial respiration (the snakes stretch their neck toward the surface for breath). Such divergence in the terrestrial habitat requirements likely explains the respective distribution of the two species of sea kraits. In the absence of beach rocks, the blue sea kraits are totally absent. Conservation programs should focus on such complex terrestrial habitats because beach-rocks are intensively used by the two snake species and by a wide cortege of organisms (crabs, sea snails etc.).

1 INTRODUCTION

"Mieux vaut prévenir que guérir"

Because resources are strongly limited, determining conservation priorities is the subject of intense debates (Caro & O'Doherty 1999, Ginsberg 1999, Mittermeier et al. 1998, Myers et al. 2000). Discussions are fertile, but the necessity for a selection between divergent options to minimize biodiversity loss and anthropogenic pressures on ecosystems also complicates decision-making. For instance, should we channel large amounts of the available founds to save the last specimens of several virtually extinct species, thereby favouring several patrimonial species? Or, conversely should we put most resources to preserve healthy ecosystems without priority towards the most threatened species? What is the optimal balance between highly focused projects limited in their scope versus broader programs without spectacular target? Similarly, are strong taxonomic biases towards few iconic species acceptable because they supposedly act as umbrellas for the whole community they belong to? Or conversely should we try to redress such bias to protect a wider variety of organisms, notably to consider the many ecosystems that do not contain popular or symbolic species? There is no simple answer to these issues; however there is little doubt that orienting excessively conservation funds towards few icons will automatically create disequilibrium towards few programs of limited span at the expense of more general ones. Although, the optimal distribution of the conservation efforts cannot be easily estimated, recent surveys suggested that a small number of vertebrate species attract disproportional amounts of resources and attention and that such bias should be redressed (Kellert 1993, Seddon et al. 2005). For instance, the extinction of popular species (e.g. birds, marine mammals) systematically generates considerable interest; meanwhile thousands of invertebrates are definitely cleaned from the planet without much compassion (Turvey et al. 2007).

Taxonomic biases are essentially explained by the combination of the influences of traditions, cultures and affective factors (Seddon et al. 2005). Beside such well-

identified obstacles, other misperceptions of the biodiversity threats further impede to set up diverse and cost-effective conservation plans. The confusion between apparent abundance and population health is a one of the potentially problematic and widespread classical mistake. Instead, early dramatic population decrease should be combated before irreversible threshold and crash. Although abundance does not necessarily reflect survival trend, it would be extremely difficult to convince the general public and the managers to allocate substantial funds to protect still relatively common, not spectacular and not commercially exploited communities of organisms despite alarming population regressions. In this perspective, the lack of information on taxonomy, life history traits, and local variations impedes estimating protection needs, and thus precludes determining an optimal allocation of the resources. Unfortunately most organisms accumulate all these burdens: they are unpopular, poorly studied, and their population trends are ignored.

This is the case for sea kraits: These reptiles forage at sea but depend on land (islets) to lay their eggs, digest their prey, and slough their skin (Heatwole 1999). Snakes are among the less popular organisms and they are killed in large numbers (e.g. up to 8,500 snakes per day in the Tonle Sap Lake in Cambodia; Crocodile Specialist Group Newsletter 20, no. 3, Jul-Sept 2001, pp. 57–58, www edition) without other consideration than the possible risk of a disequilibrium caused by the disappearance of predators controlling fishes. Although abundant in most of their geographical range (Heatwole 1999), no long-term study is available to assess sea kraits population trends. However, huge industrial exploitation of sea kraits for their meat and skin trade provoked local extinction of different populations (Bacolod 1983, 1984, 1990, Punay 1975). In addition, their foraging habitats (coral reefs) are seriously threatened worldwide (Walker & Ormond 1982, Linden 1999, Hughes et al. 2003, Riegl 2003). Therefore, a set of evidences suggests that sea kraits should be integrated into conservation programs before irreversible damages occur. The sea krait group comprises at least 8 species living in the Indo-Pacific oceans, but

most did not received precise taxonomical examination (Heatwole et al. 2005, Cogger & Heatwole 2006). Two species co-occur in the Neo-Caledonian Lagoon, one is endemic L. saintgironsi (Cogger & Heatwole 2006), the second is provisionally refereed to L. laticaudata (Heatwole 1999; Ineich & Laboute 2002). The respective life history of all sea krait species is still fragmentary documented (Bonnet et al. 2005, Brischoux & Bonnet 2007, Brischoux et al. 2007a,b). Although the diet and the foraging ecology have been studied, we have yet very few information on their terrestrial requirements, and many basic questions are open. Perhaps all sea krait species are able to use indifferently a wide variety of terrestrial habitats? Is there a strong ecological divergence between the species in terms of terrestrial habitat requirements? Where and when do the sea kraits lay their eggs? Answering to these questions is essential to understand geographic distributions, for population monitoring, and to propose conservation plans. Notably, sea kraits exhibit a strong phylopatry for their home islet, suggesting limited capacities for emigration is their usual habitat is destructed (Shetty & Shine 2002a).

The aim of this study was to describe precisely the terrestrial habitats used by the two sea krait species of New Caledonia, to determine to what extent the islets modifications can be deleterious, and thus to suggest practical and cost effective conservation actions to preserve the large populations that still occur in different places of the western Pacific Ocean (Heatwhole 1999).

2 METHODS

2.1 Study species

Sea kraits are elongate brightly banded snake species attaining approximately 1.5 m in maximum length. They forage at sea, mainly in search for anguilliform fish (Reed et al. 2002, Brischoux & Bonnet 2007). After a foraging trip, they come back to their home islet to digest their prey, slough their skin or reproduce. Typically, the snakes haul on the shore and seek for a shelter where they remain one week average

(Ineich et al. 2007; Brischoux et al. 2007b). After completion of digestion or skin sloughing, they return to the sea and they have to cross again the shore. Selecting a shelter is crucial for those ectothermic vertebrates. Although such shelters provide protection against predation (mainly avian predation, Leach 1928, Bauer & Devaney 1987), a suitable refuge must be thermally buffered and humid to allow process needed for specific activities (digestion, sloughing, vitellogenesis) and to limit hydric loss. Thus the shore of the islets is of prime importance.

2.2 Procedure

We set up a long-term mark-recaptures study in New Caledonia. Since 2002 we have individually marked more than 4,000 of sea kraits (approximately half *L. saintgironsi* and half *L. laticaudata*) and accumulated an equivalent amount of recaptures. Most of the snakes were captured by hand and kept in cotton bags until processed. They were released after completion of the measurements 1h to 24h after capture. For each individual, the species, the sex, and the age class were recorded. We measured the size, snout vent length (SVL, ±1cm) by gently stretching the snake over a flexible ruler; the body mass (±1g) was gathered with a portable electronic scale. A number of other traits have been recorded and several experiment to measure locomotor performances or anti-predator behaviours have been performed (see Shine et al. 2003a, Bonnet et al. 2005, Ineich et al. 2007 for details on the procedures). The diet and the foraging ecology of the two snake species have also been investigated (Brischoux et al. 2007a,b, Ineich et al. 2007). Sampling anguilliform fish through sea kraits revealed that these predatory fish were far more abundant and diverse than previously estimated (Ineich et al. 2007). After a successful foraging trip the snake come on land to find a refuge and to digest.

2.3 Habitat description

The perimeters (beaches) of the study islets are broadly compounded of four main structures:

(1) Sandy beaches (henceforth "sand" for simplicity). These structures are only compounded of sand dunes. As sea kraits are not fossorial species, those beaches do not provide any shelter and the snakes have to cross them for example to reach the vegetation after the bank.

(2) Stratum beach-rock (henceforth "slabs" for simplicity). These structures are constituted of sedimentary sandstone or fossil coral structures and usually form the islet basis. In New Caledonia, such structures are large flat fossil coral slabs that are exposed due to tide movements. Erosion tends to dig cup-shaped cavities that remain open and hence that are not always suitable as refuges for the snakes. However, there are natural crevices were the snakes can hide.

(3) Rock cliffs or rock overhangs, from 1.5 m to 4 m high (henceforth "cliffs" for simplicity). These structures are issued from stratum beach-rock formed during geological period with higher sea level. The cliffs and the overhangs provide few shelters (crevices or cavities). The constant erosion (owing to tides movements), that might results in cavity piercing, inevitably provokes cliff collapsing and generate some mobile beach-rocks (see below). Such structures complicate the displacements of the snakes between land and sea during successive foraging trips (Bonnet et al. 2005).

(4) Mobile beach-rocks (henceforth "beach-rocks" for simplicity). These structures are the products of long-term erosion of the slabs. Such beach-rocks are not any more connected to the original substrate. The cavities created by the irregular shape of the inferior side of those rocks and the superpositions of mobile breach-rocks provide abundant refuges. This structure was the most favourable to the sea kraits (see results), and therefore it was important to distinguish it from the three others listed above.

2.4 Study zones

A total of 9 islets situated in the southwest lagoon of New Caledonia have been sampled (Figure 1).

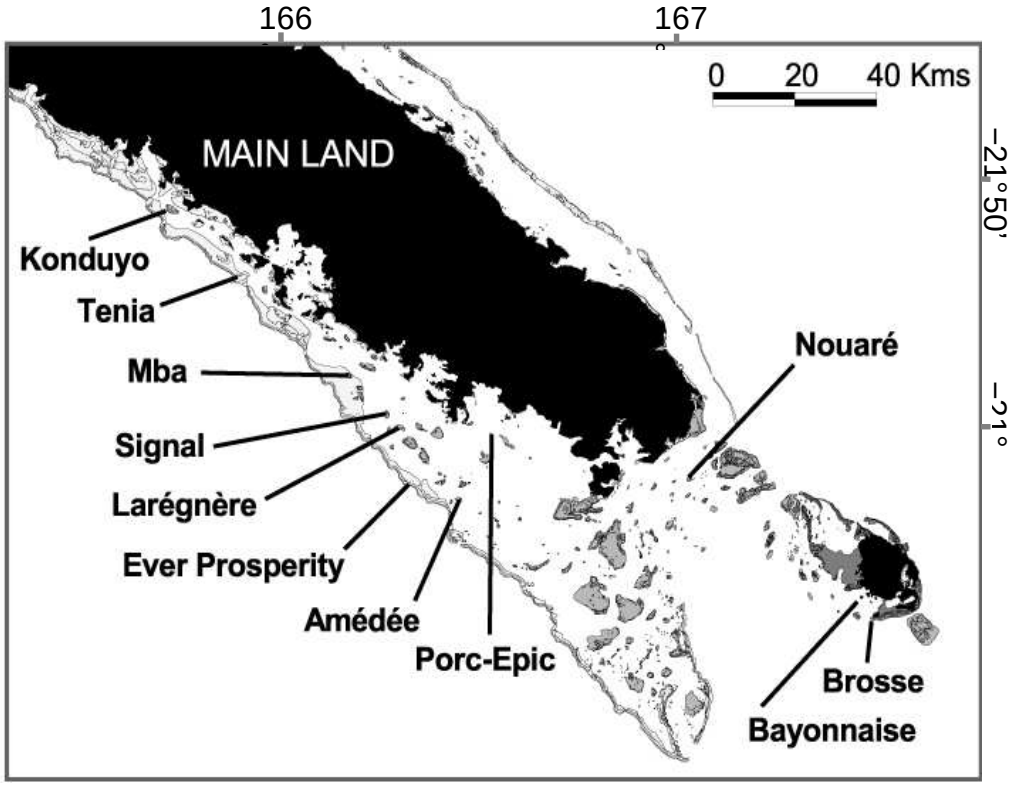

FIG. 1 - *Study area: the South-West lagoon of New Caledonia. Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by the light grey areas.*

Each islet exhibits a peculiar set of physical characteristics. For instance the elevations, vegetation, structure of the shore are unique for each site. For the current study, we focused on terrestrial habitats: the structure of the shore exploited by the sea snakes. Some islets are surrounded almost exclusively by sandy beaches, whilst in others, rocks and cliffs constitute the shore. We estimated the linear proportion of

the shore occupied by sandy beaches versus other types of potential habitats as follow. The occurrence (length) of each structure was measured based on the examination of the shore and using Google Earth free software (http://earth.google.com/) to calculate distances. A rule is available in the tool section and measurements were done in meter. The image definition of most our study sites was good using Google Earth, and it was easy to measure the length of sand areas for instance. However, it was more difficult to discriminate between the other structures (slabs, cliffs or beach-rocks), we thus we also relied on visual assessments of the study zones to discriminate between different structures. Using repeated measures of the same structures, we calculated a mean error of 5.6m (7%).

2.5 Signal island

One islet, Signal Island, was carefully monitored in order to gather precise information on the terrestrial habitat used by the sea kraits. Signal Island is a rectangular coral islet with the main axis oriented to the North (Figure 2). Therefore, four shores (sides) can be identified: sandy beaches border the south, east and north shores; the west shore is far more complex and essentially constituted by an alternation of slabs and sand covered by beach-rocks (Figure 2). The west shore extends on more than 400m from the wharf to the Signal. For simplicity, we divided the shore into 44 segments of 10m each materialised in the field using colour marks (Figure 3).

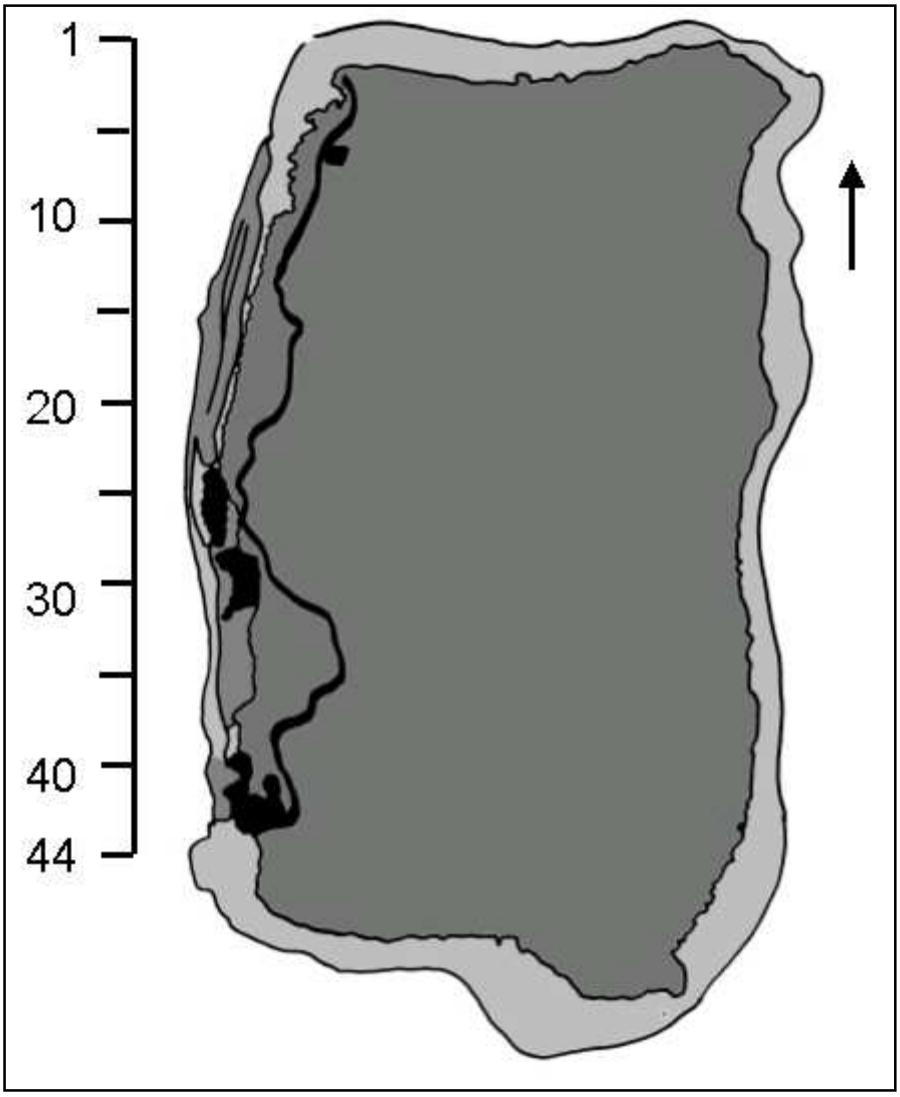

FIG. 2 - *Signal island: light grey areas represents sandy beaches, dark grey areas represents vegetation. On the west shore specifically, dark grey areas represents beach-rocks (stratum slabs and mobile beach-rocks, see figure 3 for details). Rock boulders are represented by black patches. The black line represents the tourist pathway. The scale indicates the 10m long shore segments.*

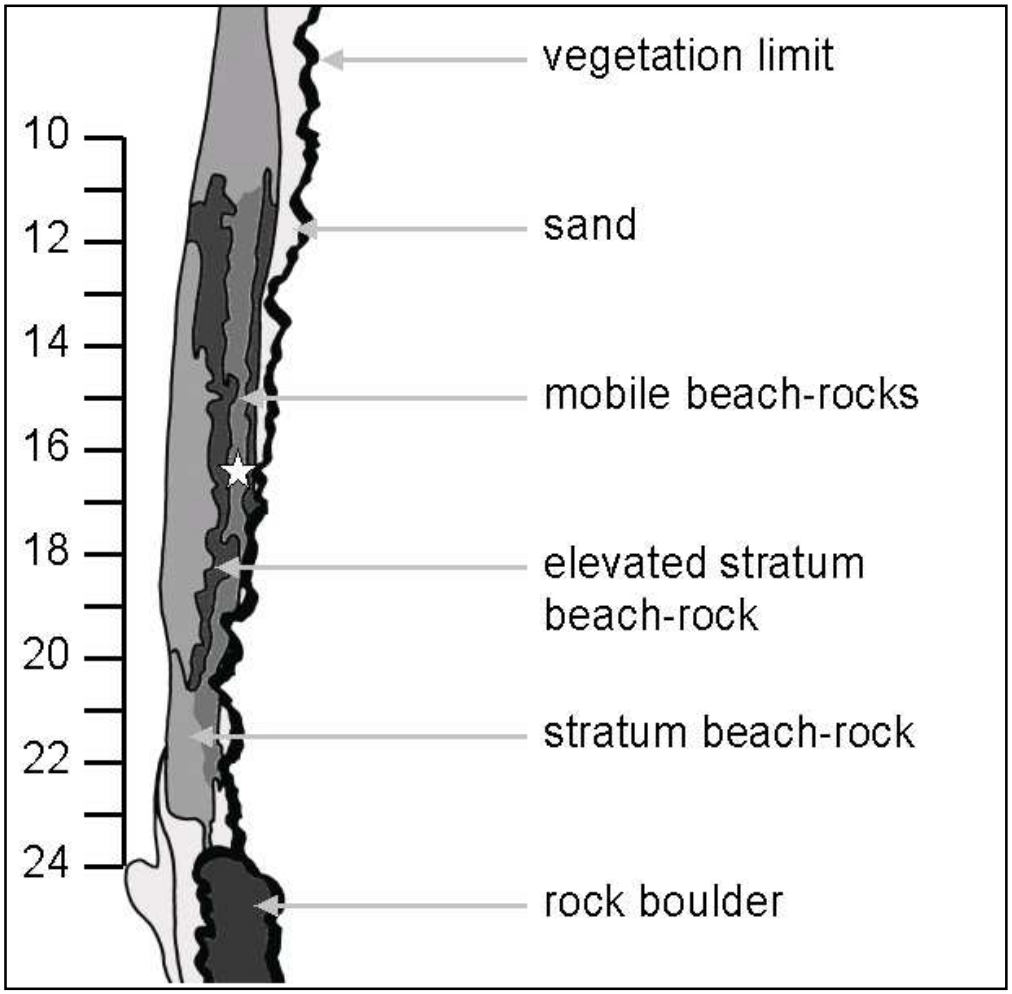

FIG. 3 - *Details of the west shore of Signal island. The scale indicates the 10m long shore segments. The star highlights the segment 16 were most of the snakes were found sheltered under mobile beach-rocks. See text for details*

2.6 Populations sizes of *L. laticaudata* and *L. saintgironsi* on Signal Island

Snakes typically exhibit marked time and inter-individual heterogeneities in the probability of capture, accurate population size estimates require to take into account these factors (Bonnet & Naulleau 1996; Bonnet et al. 2002). During a long field session, 58 consecutive days on Signal Island, the main assumptions to perform population size estimates were met (Otis et al. 1978). On average sea kraits alternate foraging trips at sea with resting periods on land on a two-weeks basis. This means that during short time surveys (i.e., <1 week), many animals are captured repeatedly because they remain on land whilst roughly half of the snake population evades sampling. Therefore, short time sampling sessions tend to miss most of the characteristics of the time-heterogeneity in the probabilities of capture, generating a risk of underestimating the whole population size. The influence of migration and mortality did not complicate the estimates. Indeed, the snake populations were considered as closed because sea kraits tend to be philopatric (Shetty & Shine 2002) and survival is high if calculated during a less than 2 months period (Bonnet et al. 2002). Population size estimates were performed separately of each species of sea kraits using CAPTURE program software (Otis et al. 1978). Signal Island supported an average of 4,087 individual snakes (1,700±96 *L. laticaudata* and 2,387±264 *L. saintgironsi*, FB, XB unpublished data).

2.7 Environmental thermal conditions

We measured the thermal conditions of the various environments available for the sea kraits on the islets. We used rubber tubes filled with seawater to mimic a snake thermal inertia (snake model, H Lelièvre & X Bonnet unpublished data). Temperature loggers (ACR SmartButton Data Loggers, sampling rate: 5 min, ±0.5°C), were placed inside each snake model. We recorded the thermal profiles of the environment during three consecutive days (typical summer days). Thermal

conditions were recorded in the open (the models were positioned just above the beach in the full sun), under a beach-rock located in the inter-tidal area (segment 18), under a beach-rock placed over dry substrate (beyond the high tide limit, segment 30), inside a sea bird burrow (2 m deep, near the tourist pathway), under a big rock boulder (beyond the high tide limit, segment 30) and under water (recovered by 10cm of water at low tide). The snake models recording the thermal conditions under beach-rocks were positioned under large beach-rocks (upper limit of our lifting ability).

2.8 Presence of sea kraits under beach-rocks

On the main study site, Signal Island, we performed 7 transects (4 in November-December 2005 and 3 in December 2006) during which we randomly lifted 695 beach-rocks. The sampling was more intense in the zones where the beach-rocks were the most abundant (Figure 3, 7). In the course of a given survey, each beach-rock was examined only once, and the total number of beach-rock present on the site was of several thousands. Therefore, our sampling was not exhaustive. We were also limited by our ability to move large beach-rocks, and for instance we totally ignored the boulders from the chaos. Similarly, we neglected the small stones. Each beach-rock lifted was measured for the three main dimensions (L/l/W). The precision was variable because the size and the shape of the beach-rocks were highly variable too. The error was broadly estimated around 15% for the linear measurements. In practice, the analyses using the main length (L) led to similar results than those using various combinations (L*l*h for instance), thus only the formers are presented. The temperatures of the upper and lower surfaces of the beach-rocks were recorded simultaneously to rock lifting using a laser thermometer (Raytek MX2) and targeting three different points for each surface to calculate a mean value. We attempted to capture all the snakes present under the beach-rock; the species, sex and age class were determined (Brischoux and Bonnet 2007). The beach-rocks were immediately and carefully repositioned to limit disturbance.

Overall, we lifted beach-rocks in 32 shore segments over the 44 available because some segments were compounded only of sandy beaches or of large boulders that could not be lifted.

3 Results

The analyses first focused on Signal Island where abundant and detailed data on the distribution of the snakes between different microhabitats have been collected.

3.1 Broad distribution of snakes on Signal Island

We first limit the analyses to the snakes observed visible in the field, either coming ashore from the sea (usually after a foraging trip; Brischoux et al. 2007), crawling on the substrate, or more or less immobile in the open (e.g. basking in the sun, during mating). Therefore, we first ignored the snakes found sheltered under beach-rocks.

On Signal Island, the yellow sea kraits (*L. saintgironsi*) were observed all around the shore. They have also been regularly spotted inside the island, notably along the tourist pathways, N=122 *L. saintgironsi* versus N=4 *L. laticaudata* (Figure 2). All the blue sea kraits (*L. laticaudata*) have been captured in the west shore, and essentially in the segments covered with mobile beach-rocks. Such clear segregation led to significant differences comparing the proportion of snakes from each species observed in the west versus the three others sides of the islet (46% of *L. saintgironsi* on the west shore versus 100% on the 3 other shores pooled; χ^2=82.48, N=5447, P<0.001). Because the west side of Signal Island was apparently the only one to offer suitable habitat to both species of sea kraits, we focused on this section. Therefore most of the captures occurred on the west coast. We emphasise that such bias due the greater catchability of the snakes on this side of this island that oriented our searching effort did not impede our ability to examine which habitats are the most suitable for the snakes. Broadly, the west rocky shore was an excellent habitat for

both species of sea kraits; the rest of the shore was visited only by a limited number of *L. saintgironsi* snakes (for example the maximal number of snakes observed over a single survey were respectively of 30 individuals on the west coast versus 9 on the three other shores pooled).

3.2 Precise distribution of the snakes on the west shore of Signal Island

Considering the 10m long segments along the shore, both species tended to display different distribution (χ^2=286.33, N=796, P<0.001, Figure 4). Even at a small spatial scale, both species were mostly observed in rocky areas; and *L. saintgironsi* was captured more often than *L. laticaudata* on sandy segments (16% versus 11%, Figure 4, compare with Figure 3). Such fine scale heterogeneous distributions suggested a tight association between the structure of the microhabitats (e.g. presence of beach-rocks) and the occurrence of the sea kraits. These results incited us to perform a closer zoom on the beach-rocks that were attracting for the snakes.

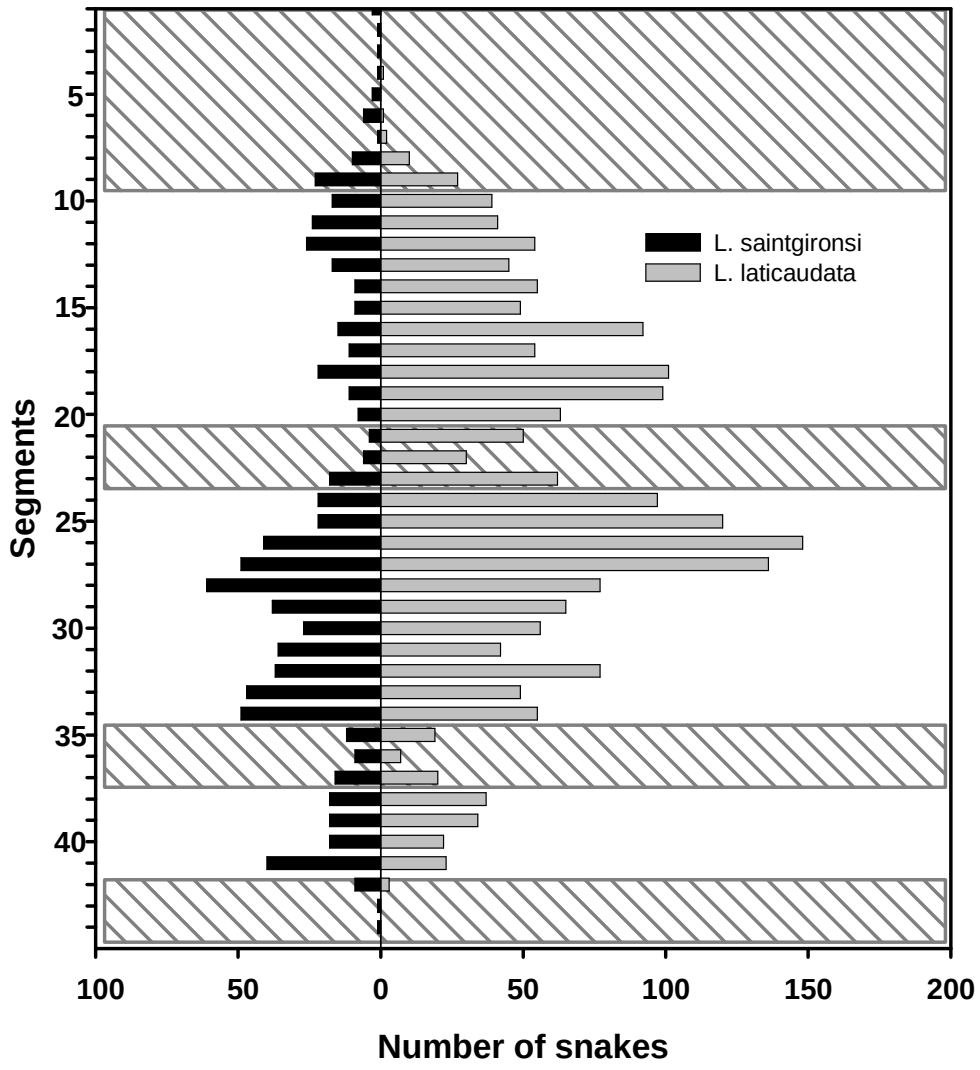

FIG. 4 - *Number of snakes captured per shore segments. Hatched boxes represent segments with a high proportion of sandy beaches. Black bars and grey bars stands for the numbers of* L. saintgironsi *and* L. laticaudata *respectively.*

3.3 Influence of the distribution and dimension of the beach-rocks on snakes

The following analyses focus on the snakes found sheltered under the beach-rocks lifted during 7 surveys. Among the 695 beach-rocks lifted, 116 were occupied by 207 snakes. Twenty-eight snakes escaped quickly and remained unidentified; the 179 others were captured and examined. One species, *L. laticaudata* was overrepresented: N=165 *L. laticaudata* versus N=14 *L. saintgironsi* (using the expected proportions of snakes based on the population size estimates; χ^2=146.84, P<0.01). The proportions of females and juveniles *L. laticaudata* were greater among the snakes sheltered compared to the snakes visible in the open (effect of sex: 33% of females under rocks [N=187] versus 19% visible [N=4,221], χ^2=23.05, P<0.01; effect of age 38% of immature snakes sheltered under rocks [N=186] versus 14% visible [N=4,207], χ^2=84.45, P<0.01).

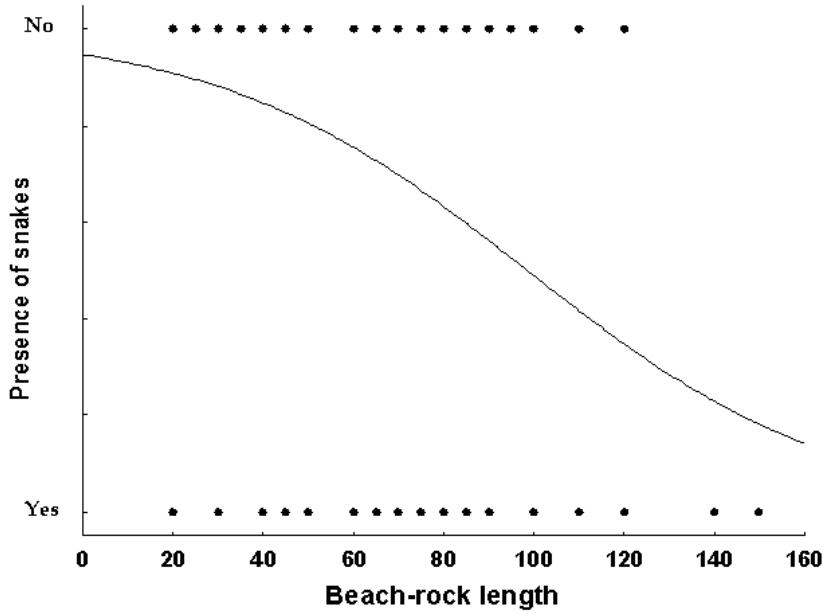

FIG. 5 - *Presence of sea kraits under beach-rocks. Most of the snakes were found under bigger rocks. See results for details on the logistic regression.*

We observed snakes only under the beach-rocks larger than 20cm in length. Disregarding the smaller beach-rocks (L<20cm, N=9), we found a positive relationship between beach-rocks size and the probability to find a snake (Logistic regression with the occurrence of snakes as the dependent variable and the dimension of the beach-rock as the predictive variable: χ^2=14.08, P<0.01; Figure 5). There was also a significant positive relationship between beach-rock size and the number of sheltered snakes (Spearman rank correlation r_s=0.12, P<0.05, N=686). However, a graphical inspection of the distribution of the data revealed that such effect despite its significance was very weak (Figure 6). Not only the data were extremely scattered, but also the largest beach-rocks did not shelter the highest number of snakes (Figure 6).

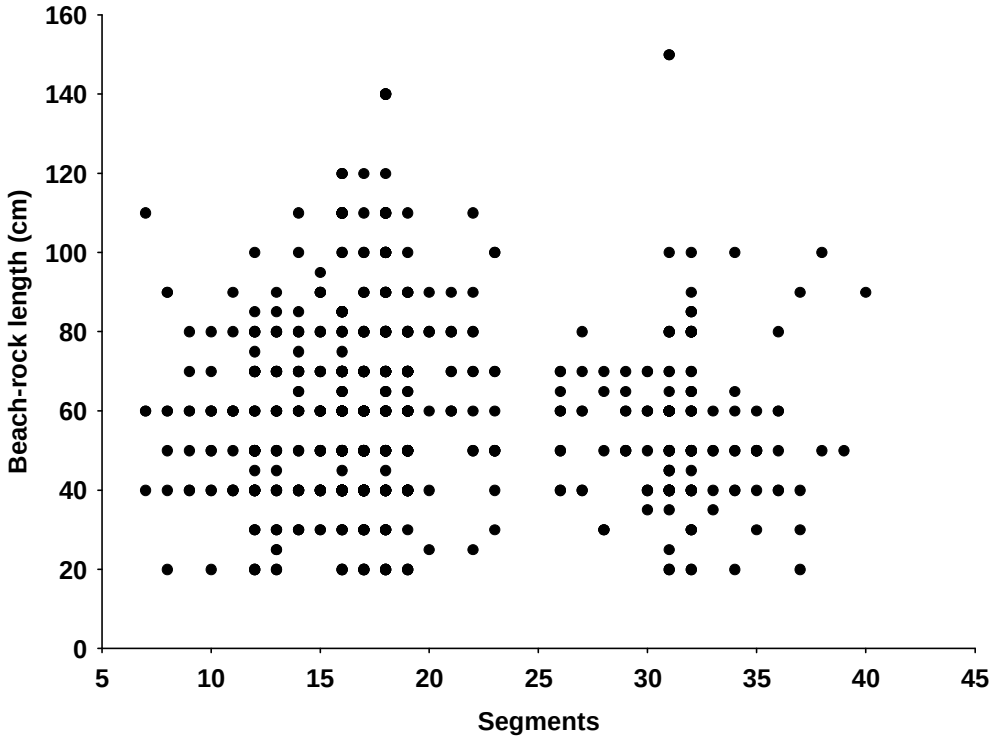

FIG. 6 - *Distribution of the size of the beach-rock lifted for each shore segments. The gap around segment 25 was due to a rock boulder.*

Therefore, we examined the possible influence of other parameters. The dimensions of lifted beach-rocks were relatively homogeneous along the shore (i.e. there was no correlation between the 10m-segments and the size of the beach-rocks; Spearman rank correlation r_s=-0.03, P>0.05, N=695). The abundance of the beach-rocks we were able to lift was variable along the shore (Figure 7).

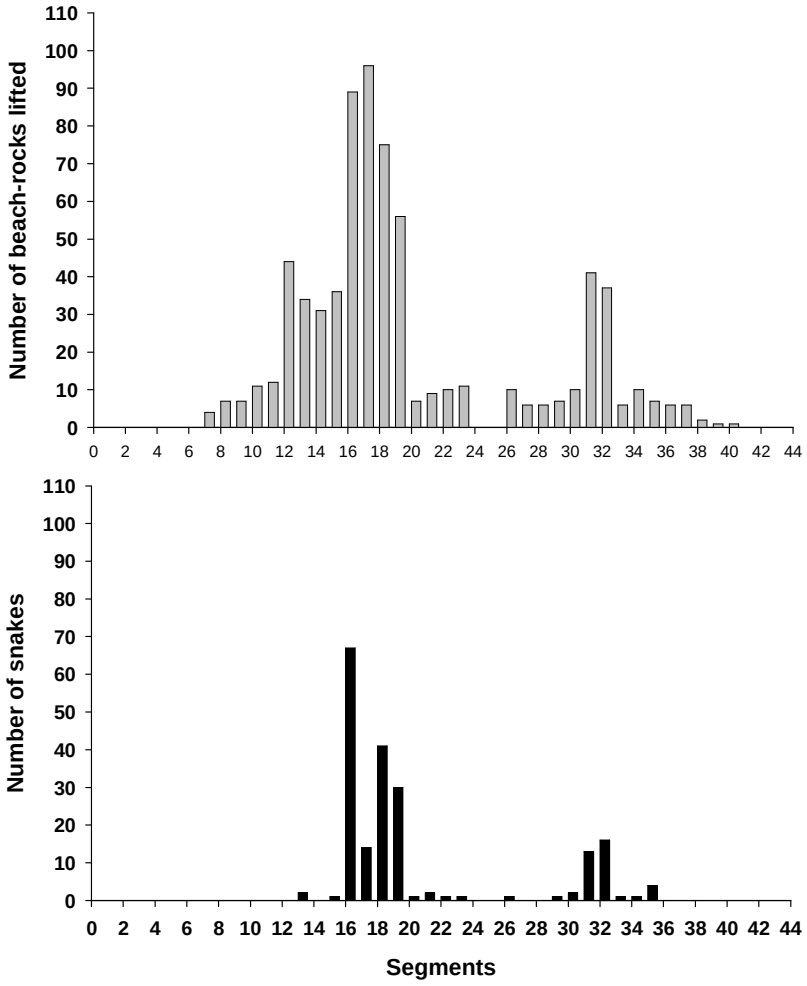

FIG. 7 - *Distribution of the abundance of rock lifted per shore segments (upper figure) and distribution of number of snakes found under the lifted beach-rocks (lower figure).*

As a consequence, the numbers of snakes found sheltered followed broadly such distribution of the beach-rocks (Figure 7). However, the snakes tended to select several beach-rocks (Figure 7). In other words, the numbers of snakes found sheltered did not follow the availability of the beach-rocks; instead the sea kraits selected few 10m-segments (i.e. 16, 18, 19, 31 & 32) corresponding to two main zones (Figure 2, 7). Theoretically, we should have observed one snake every six beach-rocks lifted, such ratio enabled to calculate an expected number of snakes per segment varying from 0 to 27. Comparing such expected distribution against the observed distribution (varying from 0 to 67), we found a significant difference (χ^2=176.47, P<0.01). Therefore, the snakes tended to aggregate under several peculiar beach-rocks.

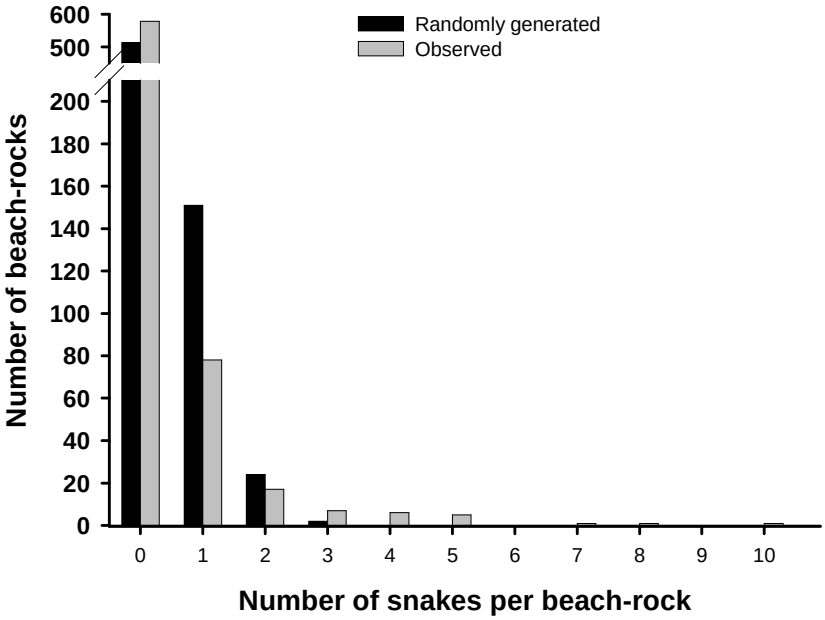

FIG. 8 - *Distribution of the number of snakes found under each lifted beach-rocks. The randomly generated distribution is the mean of 200 random distribution. Theoretically, 3 snakes under one beach-rocks is the maximum value. The observed distribution show that up to 10 snakes can co-occur under a single beach-rock.*

To further test this hypothesis we generated 200 random distributions of the number of snakes that could be observed under each beach-rock: for that the 207 observed snakes were randomly allocated among the 686 beach-rocks. On average, the resulting maximal number of snakes under a given beach-rock was different from the observed distribution (χ^2=96.30, P<0.01; Figure 8). In the field, a greater than expected proportion of beach-rocks contained no snake, a lower than expected number of rocks contained a single snake; but a greater than expected of them sheltered several snakes (up to 10 snakes under one beach-rock).

3.4 Thermal characteristic of the beach-rocks

We compared the thermal profile of snake models positioned in the open versus placed in different potential shelters or in the seawater. A graphical inspection of the data reveals clearly that a snake cannot stay in the open (the lethal body temperature is <40°C in snakes) during the day and that the temperature cool down sharply at night (Figure 9). The puffin burrows and the very large boulders provided buffered thermal conditions. The large beach-rocks just beyond the high tide limit remained dry and exhibited high daily temperatures (close to critical temperatures); thus smaller beach rocks would have almost certainly over passed the lethal temperature threshold. By contrast various size beach-rocks positioned in the inter-tidal zone remained buffered (due to the evaporation of the water from the very porous rock) and tended to follow the thermal profiles of the seawater. The most thermally buffered beach-rocks were immerged at high tide. This situation, although favourable in terms of ambient temperatures and humidity posed a problem for the snakes that rely on aerial respiration.

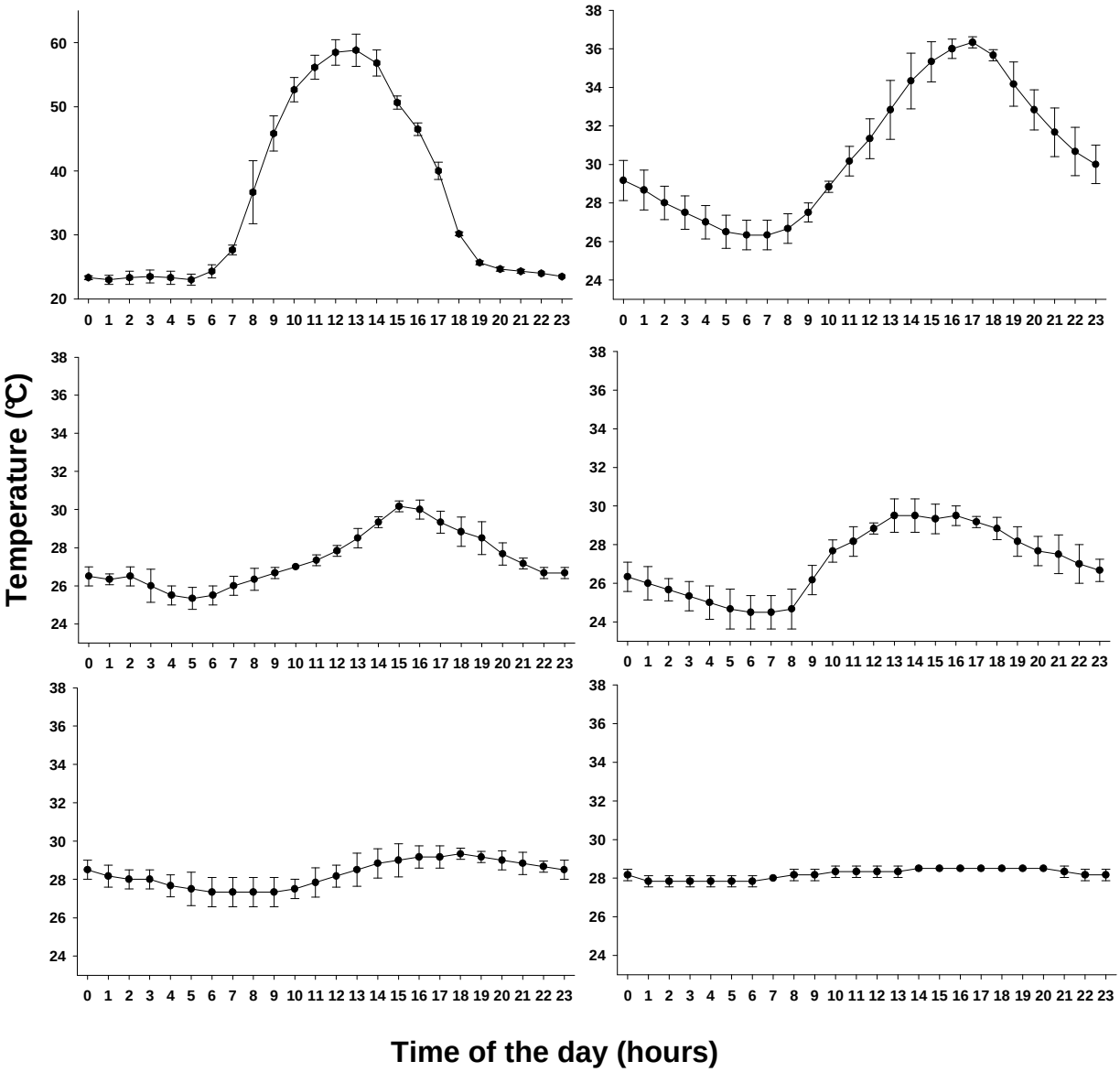

FIG. 9 - *Thermal condition in various types of environments. Values were pooled from 3 typical summer days. For simplicity we kept only one temperature value per hour. From top to bottom and from left to right: in the open (note the different scale in comparison to the other thermal profile), under a beach-rock beyond the high tide limit (segment 30), in the seawater, under a beach-rock positioned in the inter-tidal zone (segment 18), under a big rock boulder (segment 30), and inside a sea bird burrow (2m deep).*

3.5 Respiratory behaviour

Two evidences suggested that the sea kraits (essentially *L. laticaudata*) remained submerged under the favourable beach-rocks at high tide. Firstly we observed many snakes sheltered when we lifted partly or fully submerged beach-rocks (see above); second we never observed massive displacements of the snakes leaving the beach-rocks in the front of the elevation of the water level. Close observations of the beach-rocks occupied by the snakes enabled to describe a novel behaviour that specifically occurred at high tide and solely in *L. laticaudata*. Regularly, the snakes sheltered under submerged rocks stretched the front part of the body to reach the surface of the water whilst the rest of the body (>2/3 of the whole body) remained under cover. They released few bubbles, pierced the surface and took a quick breath (the noise of the sea kraits breathing through nostril valves is very distinctive), and then retired back rapidly under shelter. The sea kraits can hold their breath for long time periods (>2h; Brischoux et al. 2007c), however the typical time interval between two breaths is approximately of 4-5 minutes (pers. obs.; we observed one individual sheltered under a beach rock that stretched its head to breath 10 consecutives times with a mean interval of 1.37min). During two 30 minutes focal observations performed at high tide in the shore-segment where the *L. laticaudata* tend to aggregate (segment 16; Figure 3) we observed 45 snakes extending their neck for breathing without leaving their shelter. We also observed 15 snakes moving between shelters under water. The maximal water level compatible with the neck-stretching-breathing technique was approximately of 25 cm above the basis of the beach rocks depending of the size of the snake. Interestingly, such water level was precisely attained at high tide in the most favourable segments. The beach-rocks both close to the shore and uncovered by the sea at low tide, but nonetheless neglected by the *L. laticaudata*, typically fell into two categories: either submerged by more than 30cm of water (sometimes >50cm) or not submerged at all. The first category corresponded to the rocks that accumulated heat and that remained dry

during the day (Figure 9); the second category corresponded to the rocks that would have constrain the snakes to leave regularly their shelter for breath. Overall, the zones of the shore favourable to the L. *laticaudata* combined at least two important characteristics: 1) the occurrence of beach rocks that provide shelters is indispensable; 2) the sea must cover the rocks only few hours at high tide to buffer thermal (and very likely hydric) conditions without impeding aerial respiration.

3.6 Broad distribution of snake species between the studied islands

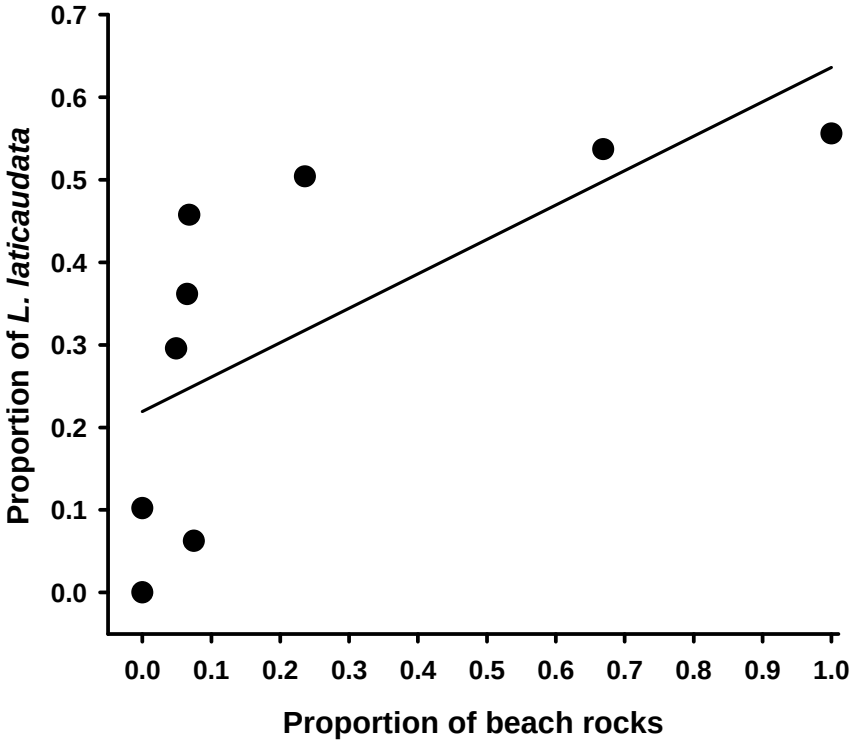

FIG. 10 - *Proportion of* L. laticaudata *in relation to the proportion of beach-rocks along the shore of 9 different islets. We found a significant association between* L. laticaudata *and beach-rocks. See results for details.*

For these analyses we relied on crude estimates of the availability of the terrestrial habitats suitable (shore structures) for the sea kraits. The results above suggested that *L. saintgironsi* was able to exploit various types of shores, including sandy beaches; whilst *L. laticaudata* was dependent on the presence of beach-rocks. Therefore we expected that the proportion of each snake species would be influenced by the characteristics of the shore of each islet studied. We found a significant relationship between the proportion of the shore composed by beach-rocks and the proportion of *L. laticaudata* (r_s=-0.82, P<0.05, N=9; Figure 10).

4 Discussion

Our results indicate clearly that the structure of the terrestrial habitat, notably the occurrence of refuges, plays a key role for two species of sea kraits. The fact that the presence of terrestrial shelters was essential for both species of snakes conforms well to the general ecology of most reptiles; the necessity to protect refuges for snake conservation is therefore patently obvious (Webb & Shine 2000 and references therein, Shine & Bonnet 2007). However, such type of banality in the conclusions remains too vague to be transposed into operational actions. In the absence of meticulous behavioural observations, the notion of "shelter" remains very imprecise; for instance bird burrows provided the most buffered thermal conditions (a key factors for reptiles) and both sea krait species use them (unpublished data using endoscopes). However, conservation plans based on the presence of bird burrows alone would be efficient for only one species (*L. saintgironsi*) because the other (*L. laticaudata*) mostly depends on peculiar beach rocks positioned in the inter-tidal zone. In addition, the fine scale data gathered on Signal Island enabled to better understand the distribution of the sea kraits at a large geographic scale; suggesting that eco-physiological characteristics associated to precise environmental constraints determine the respective requirements of each species. Indeed, although previously considered as relatively similar species (Heatwole 1999), recently

acquired data revealed important ecological differences between *L. saintgironsi* and *L. laticaudata* (Brischoux et al. 2007b, c).

L. saintgironsi was observed in various places around and within the islands, and was able to exploit a vast array of terrestrial refuges such as puffin burrows, holes in the root trees, large logs, debris, human habitations, and a range of types of beach-rocks. This species exhibits well-developed abilities to move on land, to climb steep cliffs (Bonnet et al. 2005), and is regularly found 40m above the sea level (e.g. on Porc-Epic Island). By contrast, *L. laticaudata* is a poor climber species that crawls slowly on land (Bonnet et al. 2005); it is almost systematically observed on the shore, and essentially in the close vicinity of the beach rocks that are at least partially submerged at high tide. A greater skin permeability of *L. laticaudata* compared to *L. saintgironsi* has been documented (H. Lilywhite pers. com.). Such difference reinforces the divergence in the habitat use between the two species of snake: the marked skin permeability of *L. laticaudata* promotes underwater respiration (e.g. facilitating uptake of oxygen; H. Lilywhite pers. com.), but also increases dehydration risk (Lilywhite pers. com.). The marked desiccating influence of strong southeast trade winds provides an additional factor to explain why *L. laticaudata* was only observed in the well-protected west side of Signal Island. Such effects are likely important because on average sea kraits remain on land during long time periods (one week on average to complete digestion skin sloughing or to lay eggs for example), and the opportunity to drink fresh water are extremely limited (see below). The physiological characteristics of *L. laticaudata* may well constrain this snake to shelter into thermally buffered and wet refuges; inter-tidal beach rocks offer both, the sea water provides relatively stable temperatures and humidity. The snakes select the beach rocks that nonetheless enable aerial respiration without extensive movements between places as indicated by the novel neck-stretching breathing behaviour we observed; otherwise, the benefits of the shelter would be compromised. Overall, sharp contrast in the abilities to exploit terrestrial

environments explains the strong divergences in the sheltering capacities of the different islets we investigated.

Importantly, the occurrence of beach rocks is the smallest common denominator with respect to the terrestrial requirements of the two snake species. Indeed, *L. saintgironsi* uses intensively the large boulders areas (i.e. chaos of large coral rocks) and the fields of beach rocks distributed over and 20-m beside the shore (Figure 2). There is no fresh water on the islets and during rainfalls the sea kraits leave their shelter to drink form puddles (unpublished data). Over more than 120 fieldwork days, we observed 7 rainfalls and 11 drizzling days; at these times, large numbers (hundreds) of *L. saintgironsi* emerged from the chaos to benefit from the precipitations, thereby revealing the massive use of these areas as terrestrial refuges (unpublished data). To drink during rainfalls, we also observed many *L. laticaudata* leaving the inter-tidal beach-rocks and the refuges situated immediately above the shore (within a narrow 20m fringe, including the chaos in contact with the upper tide limit). We also suspect that the chaos made of large boulders are used as laying sites: we base this conclusion on the fact that many pregnant females and neonates have been captured in these areas. Overall, fields of beach-rocks extending from the inter-tidal zone to a 10-20m-depth fringe above are likely to provide suitable refuges for both species.

Proposals for conservation plan

Our results enabled to identify precisely beach rocks as a key-terrestrial habitat for both species of sea kraits. Unfortunately, in contrast to muddy and sandy shore (Kathiresan & Qasim 2005), modest rocky elements are rarely appreciated as important components. In many tropical islands, tourism occupies a central place in the economy, and sandy beaches are far more attractive compared to rock fields; in New Caledonia several beaches have been subsequently heavily transformed and now, do no provide any shelter (Brischoux & Bonnet 2007). The perception of an ideal clean tropical beach is strong; artificial concrete rocks are associated with a

negative image whilst sandy beaches would appear as more natural. However, on several islets (i.e. Amédée Island, an intensively anthropised area), *L. laticaudata* concentrates in two highly localised and small artificial areas: several concrete blocks that stabilise the posts of the wharf, and a sea wall offer valuable shelters in an otherwise sandy islet. Cleaning or polishing such artificial constructions to restore a supposedly more natural image would entail the disappearance of *L. laticaudata.* Therefore, it is important to not only protect natural fields of beach rocks but also to retain artificial concrete structures that partially compensate for the "cleaning" of many other areas. In the islets of New Caledonia we investigated, the shore areas favourable for the two species of sea kraits (indispensable to *L. laticaudata*) are not abundant (Signal Island being one of the best islets with a large and complex beach rocks field). Such situation is both a bless and a curse. The main danger is that the rarity of the favourable areas renders them vulnerable to perturbation (no alternative refuges being available). The major advantage is that conservation planning can be precisely oriented towards few well identified targets. When on land, sea kraits tend to move at dusk and during the first hours of the night. The rest of the time they tend to remain sheltered in their terrestrial refuges (or are at sea). The limitation of mass tourism on the beaches to daily hours, as practiced on Amédée Island (thanks to the regulations imposed by the functioning of a major lighthouse), is compatible with the snake movements from or to the sea. Although Amédée Island is the most intensively visited islet of New Caledonia, this site nonetheless shelter large populations of sea kraits.

Not only is it essential to conserve beach rocks, but also experiments are conceivable. Adding artificial beach rocks would be the most evident option. Interestingly, concrete slabs would offer valuable protection for the birds to; many burrows collapse under the feet of carefree tourists. On the other hand, several puffins dig their nest under large flat rocks, resistant to human frequentation, and the snakes also used such burrows. Overall we propose several simple and cheap

recommendations that can be applied at a large scale over the distribution area of the sea kraits:

1) Protection of the beach rocks fields (either natural or artificial) where populations of sea kraits occur.

2) Prohibit the beach-rock lifting, for example for sea snail harvesting, notably because the hunters do not move the rocks carefully and do not put them back.

3) Limit, or organise, mass tourism at dusk when the zones favourable for the sea kraits overlap with very popular places (e.g. Amédée Island). For example, the construction of pontoons should not cause major troubles whilst the creation (or "cleaning") of sandy beaches would be disastrous.

4) Test artificially created beach rocks fields (e.g. using concrete slabs or rocks) to promote the installation of populations of sea kraits. If successful, this technique would be very useful to attract threatened populations of sea kraits into natural reserves more easily monitored, or to help restoring populations after massive hunting.

5) Educational programs organised in the field are very effective in educating people on the necessity to conserve both habitats and species. Actions revolving around beach rocks provide a simple and cost effective way to reach such essential target for long-term conservation plans.

Beside sea-kraits, the protection of the beach rocks situated in the inter-tidal zones is likely essential for a vast cortege of organisms belonging to a wide range of taxa. Many algae, arthropods (crabs…), molluscs (chitons, sea-snails…), echinoderms (sea cucumbers, ophiurids…), fish (moray eels, gobies…), or birds (e.g. bridled terns nest on large beach-rocks) for instance occur specifically on this narrow fringe of the shore. In addition, beach-rocks protect the shore from erosion and therefore enable the maintenance of the next fringes of habitats (plant names…). New Caledonia is considered as a biodiversity hot spot that deserves important

attention (Myers et al. 2000); there is little doubt that the shore of the islets should be considered as a hot-spot *per se* and need specific conservation measures.

LES CONTRAINTES DU MILIEU INSULAIRE

Thirsty sea snakes forsake their shelter during rainfall

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Abstract. Vertebrates living in dry and salty habitats spend significant amounts of time and energy to maintain their hydro-mineral balance; any opportunity to drink fresh water should reduce such expenses. However, in natural situations drinking is not always an easy task. For instance, to find fresh water, individuals can be forced to leave their shelter and to move in open areas. To examine this issue in the field, we used a very large data set (> 9,000 captures and recaptures) on amphibious sea snakes that face periodic droughts. The study was carried out on different islets in the lagoon of New Caledonia. During dry weather, sea kraits remain concealed most of the time under rocks or within burrow. They tend to select precise time windows to move rapidly between the sea and the land. Rainfalls triggered massive disruptions of this rhythm: many snakes quickly forsook their shelter to drink in the open, and remained almost motionless until satiety. Interestingly, they adopted specific and unusual postures to drink: perched on the top of rocks to benefit from the running and less salty water during downpours, they drunk the droplets attached to the vegetation during drizzles.

KEY WORDS: drinking, *Laticauda*, sea snakes, water balance

1 INTRODUCTION

In many species, the maintenance of the hydro-mineral balance imposes strong behavioural constraints (Bradshaw 1986, 1997). Animals that face hot and dry conditions must remain sheltered within burrows over long time periods, thereby trading water saving against other activities such as mate searching or foraging. Any opportunity to drink fresh water should relax such constraints. Although drinking is vital for most terrestrial or aquatic animals (Bennett et al. 1986, Schmidt-Nielsen 1990), this is rarely a simple task in many natural situations. Drinking in the open forces individuals to leave their shelter, sometimes to undertake long-trips, and therefore increases energy expenditure and the risks associated with overheating and predation (Shepherd 1981, Wehner et al. 1992, Klaassen 1996, Bergström & Skarpe 1999, Georgiadis et al. 2003, Scholz & Kappeler 2004). Even for animals living close to fresh-water bodies, drinking can be problematical. Many predators wait in ambush position around ponds, riverbanks and under the water surface (Cade 1965, Beck et al. 1973, Dill 1977, Shepherd 1981, Ferns & Hinsley 1995, Shine et al. 2004b). Although dry and/or salty habitats pose such type of physiological and behavioural challenges to a wide array of organisms, these issues remain poorly documented under field conditions.

Ecological studies that investigated drinking behaviour *per se* are scarce, limited to few species of birds (Cade 1965, Fisher et al. 1972, Ferns & Hinslay 1995), mammals (Laurenson 1995, Starin 2002), and often restricted to some descriptive parameters (Cade et al. 1966, Rode et al. 2003). In the current study, we took advantage of the ecological situation faced by two species of amphibious sea snakes (sea kraits). They use both marine and terrestrial environments, essentially the sandy shore of many coral islets in the Pacific Ocean (Heatwole 1999). Freshwater is virtually absent in both habitats: in most coral islands there are no water bodies or rivers and rainfalls are scarce whist the sandy substratum does not hold the rain. Nonetheless, sea kraits have been observed drinking running rainwater (Guinea 1991). This suggests that sea kraits rely, at least partly, on the absorption of

freshwater to preserve their hydro mineral equilibrium. More generally, for air-breathing species that live in dry/salty habitats, the maintenance of the hydro-mineral balance entails significant energy expenditure (Schmidt-Nielsen 1990) but freshwater availability for drinking is generally ephemeral. Therefore, climatic events during which water becomes available (e.g. rainfalls) should influence the time budget and the behaviours of the individuals exposed to long periods of drought. In this context, several predictions can be proposed.

Individuals should rapidly drink freshwater as soon as possible. Therefore, precipitations should rapidly modify the activity patterns. For example, hidden and presumably well-protected animals should emerge from their shelter to drink from puddles.

Most individuals should quickly return under shelter after completion of drinking, notably to avoid predation and to benefit from the mild climatic conditions of the burrows.

Individuals should select the best quality water. For instance preferring freshwater instead of brackish water to reduce the time and physiological efforts necessary to restore their water balance. This should be especially important when the access to fresh water is limited in time.

2 METHODS

2.1 Study species

Sea kraits (sea snakes) forage in the ocean, but return to land to digest their prey, slough their skins, rest and reproduce (Heatwole 1999, Brischoux & Bonnet 2007, Brischoux & al. 2007b). We studied two species, *Laticauda saintgironsi* (yellow or common sea krait) and *Laticauda laticaudata* (blue sea krait). Sexual maturity is reached at a body mass of approximately 100g (corresponding to a body size of 70cm Snout Vent Length); neonates or very young snakes usually weigh less than 50g (SVL<50cm); snakes in between these two sizes were considered as juveniles.

Sea kraits exhibit a marked tolerance to slow moving human observers; this feature greatly facilitated behavioural observations. However, they show typical anti-predator response when threatened: they hide under rocks, or flee in the sea (Shine et al. 2003a).

2.2 Study site and general survey procedures

The main study site was Signal Island, a 6 hectares flat rectangular islet and a natural reserve situated in the south-western lagoon of New Caledonia (22°17′47″S; 166°17′34″E). It is a typical flat islet covered by a sclerophylic forest, characterized by irregular summer rainfalls and the absence of water bodies (natural or artificial). Strong trade winds generate important spray most of the time.

Since 2002, we spent 140 days on Signal Island. Over that period, we performed 408 standardized surveys, essentially along 450m of west shore that is relatively protected from the main trade winds. Each survey lasted 30 minutes to 1 hour, depending upon the number of observers and upon the number of snakes encountered. The zone monitored was composed essentially of flat beach rocks (80%) alternating with small sandy beaches (20%). Two block fields (roughly L-20, l-5m, H-2m) made of large coral boulders accumulated decades ago for lime production span between the shore and the sandy bank. Behind the beach, there is a high density of petrel burrows. Crevices, flat rocks, block fields and burrows provide many shelters for the snakes as assessed by direct observations and radio tracking. During each survey, one to five peoples walked along the shore in search for the snakes. The number of observers accelerated the process (e.g. data recording…) and shortened each survey, our walking speed varying from 0.5 to 1 km/h. Sea kraits were easily located (owing to their banded colour pattern) and captured (due to their tolerance to handling). Our searching effort was lower at night (23h00 – 5h00: total 41 surveys using head torches). Because our campsite was located within the study site, few meters from the shore, daytime corresponded to the most intensive period of monitoring of the study area: we surveyed at least one

quarter of the shore (≈100m) almost permanently from 6h00 to 17h00. During the day-phase, searching was facilitated notably because our vision was not limited to the spotlight provided by the torches. This means that all else being equal, the maximal numbers of observations should have occurred during this time slot.

For each snake found, the time and the behaviour were recorded. When a snake was seen crossing the beach, basking in the sun, mating, or immobile on the substrate, it was considered as visible. When the snake was found under a rock (or a log), it was considered as concealed. For simplicity, we classified the snakes as inactive when concealed, and active in the other cases. The sex was determined by inspection of the tail. Body mass (±1g) and body size (±1cm) were measured using an electronic scale and a flexible ruler (see Bonnet et al., 2005 for details). In most snakes, including sea-kraits, drinking is easily identifiable: the tip of the mouth is placed in direct contact with the water, slow and rhythmic movements animate the jaws in order to pump the water (Berkhoudt et al. 1994, Cundall 2000). During behavioural observations, the snakes were not systematically captured. From distance, the age and the sex of the snake can often be determined. This procedure produced the least interference with behaviours. Snake's size (hence age) can be crudely estimated by sight with a precision of 5-10 cm (5cm on small snakes, 10cm on large snakes). A test (visual estimates followed by captures and measurements) on 50 snakes showed that visual estimates correctly assigned snakes to age classes in 90% of the cases. Neonates snakes are easily identifiable owing to their very small size; similarly most of the adults are large (above 70cm, >100g) and easily classified; incorrectly classified snakes represent a small proportion (12%) of the total (e.g. large juvenile and small adults). Similarly, the sex of the adults was obtained by visual examination of the shape of the tail without capture (misclassification 4%).

Within a given survey, the risk to count twice an individual was almost inexistent because the observers were getting about linearly along the shore, far more rapidly than the snakes did. Among surveys, we could not eliminate the possibility that unidentified snakes (e.g. individuals not captured during

behavioural observations) were counted more than once, thereby generating pseudo-replicates in the data set. However, most of the observed snakes have been individually marked (N=4,714 snakes marked and 4,233 recaptures; see Brischoux & Bonnet 2007), and snake identity was checked for 93.4% of the observations. Overall, our data set includes captures, recaptures and a small proportion of unidentified animals. It was consequently possible to eliminate putative pseudo-replicates in most analyses; in practice, the exclusion of potential pseudo-replicates did not change the results.

From 2002 to 2006, during 93 days, different surveys have been performed on eight other islands of the Neo Caledonian lagoon: Îlots Brosse, Amédée, Nouaré, Bayonnaise, Larégnère, Mba, Ténia, and Porc Epic (Brischoux & Bonnet 2007). The protocol used to monitor the different populations of snakes was broadly similar for all the sites (i.e. adjusted to the peculiarities of each islet), including Signal Island. These additional data (N=2,565) provided an opportunity to assess the generality of the patterns observed on Signal Island.

3 Results

3.1 General activity patterns of the snakes

In the course of the 140 days monitoring Signal Island, we observed 6,890 snakes. Hourly counts of the total numbers of snakes observed revealed clear activity patterns (Figure 1). Marked peaks of displacements were identifiable: the snakes crossed the beach mainly at dusk and at the beginning of the night. Despite intensive searching, we observed few snakes crawling on the beach from 8h00 to 15h00. After removing the time period of low searching effort (23h00 to 5h00) and comparing the actual distribution against a theoretical homogeneous distribution of the observations, the peaks of activity led to a significantly non-random distribution of the observations (χ^2=8,572.8, df=17, P<0.001). Extending the analyses to other islets (hence increasing the total number of observed snakes to 9,144 observations)

did not change the results (Figure 1). Similarly, restricting the analyses to a single observation per individual (hence excluding unidentified individuals and recaptures to eliminate pseudo-replicates) provided the same patterns with two peaks of activities (N=2,921; χ^2=7,823.8, df=17, P<0.001). Overall, the bi-modal activity of the snakes with a minor peak early in the morning and a marked peak at dusk separated by a strong decrease of movements during the day was a robust pattern.

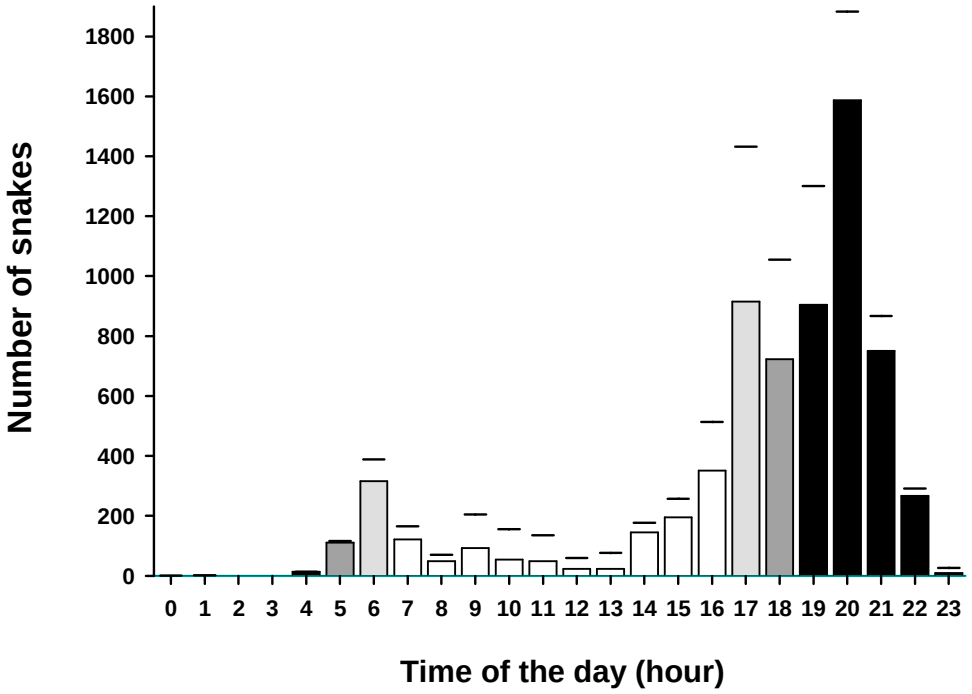

FIG. 1 - *Pattern of catchability of two species of sea snakes (*L. saintgironsi *&* L. laticaudata*) on Signal Island, New Caledonia. Each bar represents the total number of snakes counted per-hour. The grey-black colouration provides a rough scale for sunlight, from full day (white), partial darkness (grey) to full darkness (black). The line above each bar indicates the value when data from 8 other islets (see text) have been added.*

The two species, however, exhibited significant differences. Most of the yellow sea kraits (*L. saintgironsi*) started to move half an hour before the sun set; most of the blue sea kraits (*L. laticaudata*) crossed the beach later after sunset (Figure 2; comparing the two species, restricting analyses to Signal Island, to the time period of intensive searching, and to a single capture per marked individual: χ^2=1,013.1, df=17, P<0.001). Overall, the activity pattern of the snakes was strongly affected by a combination of at least two factors, the time of the day and the species.

3.2 Occurrence of rainfalls

Rainfalls occurred rarely in the study site: over a total of 221 days of fieldwork during which the weather was recorded (all study sites included), we observed one strong downpour, six rainy days, and 11 days with a fine drizzle. The strong downpour, and to a lesser extent the rains, quickly produced puddles and little streams running on hard substrates (rocks, logs). By contrast the drizzles generated droplets on the vegetation, notably on the purslanes (*Sesuvium portulacastrum*), but the formation of running water or puddles was limited (or null). For all these events, the preceding days were dry by definition; and owing to the combination of high summer temperatures with permanent trade winds we never observed the formation of dew. For instance, on Signal Island from the 21 January to the third of February 2005, no rain at all occurred and the vegetation was very dry. Therefore, during at least two weeks, no fresh water at all was available for the snakes before the tropical storm produced very abundant downpours the third of February at 17h08. Similarly, a sudden rain starting at 17h05 the 18 of January 2006 interrupted a 30-days drought.

3.3 Influence of rainfall on the activity patterns

During rainfall, many snakes rapidly left their shelter and became visible in the open (Figure 2). On average, the rain multiplied by 24 the catchability (number of

individuals observed per hour of survey) of the snakes. This effect was particularly visible as most of the rains started at a time slot of low activity (13h00 – 15h00; catchability increased 42 times); but remained particularly pronounced later (16h00-18h00; catchability increased 5 times). For instance, a single rainfall starting suddenly during the 14h00 time slot enabled to count more than 100 snakes, compared to less than 50 snakes observed during all the other surveys cumulated (Figure 2).

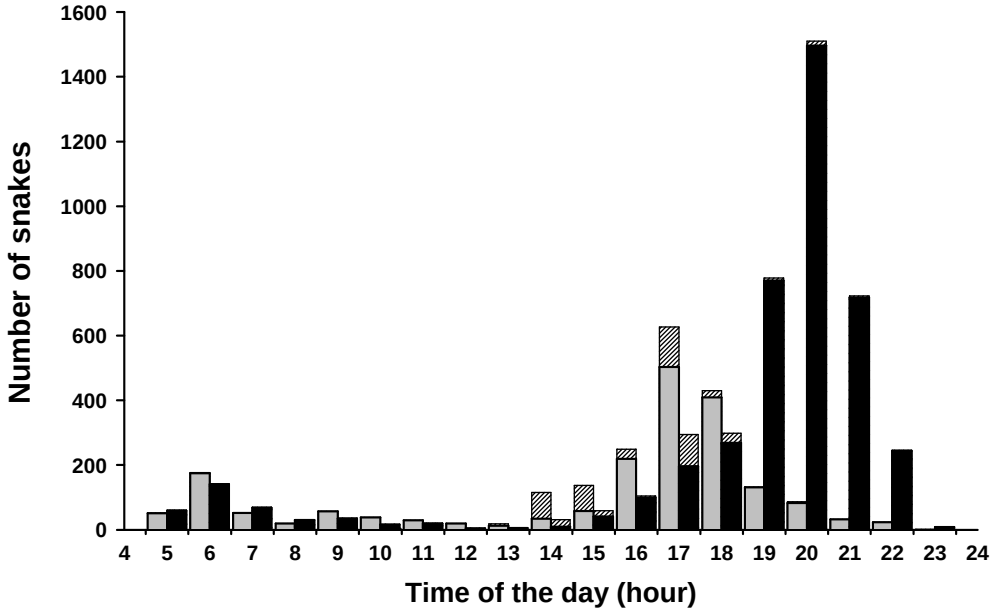

FIG. 2 - *Comparative activity patterns of the two species:* L. saintgironsi *(grey bars) versus* L. laticaudata *(black bars). This figure is limited to the time period of high searching effort, from 5h00 to 23h00 and to the snakes observed during dry weather (N=137 days). The hatched bar above the grey and black bars provide the values obtained during wet weather (rainfalls, and drizzles, shortly after the rain stopped; N=4 days).*

Comparing the proportion of snakes visible *versus* hidden during the 13h00 – 18h00 time slot when most of the rain occurred, we found a strong effect of the weather: under dry conditions 45% of the snakes (N=2,189) were hidden under

rocks. In stark contrast, during the rain, 98% of the snakes (N=490) were visible in the open (χ^2=304.9, df=1, P<0.001).

3.4 Difference between the species

We first limited the investigation to the time slot (14h00 – 18h00) that corresponds to the peak of activity of *L. saintgironsi*, but not yet to the peak of activity of *L. laticaudata* (Figure 2). The rain provoked an early emergence of *L. laticaudata*: we found 448 blue sea-kraits, essentially sheltered (74% hidden) under dry conditions but 163 individuals (6% hidden) during the same time slot under wet conditions (χ^2=229.6, df=1, P<0.001). By comparison, 890 *L. saintgironsi* were found during the dry days, but only 36% were hidden; *versus* 323 snakes (1% hidden) during the rainy days (χ^2=147.5, df=1, P<0.001). Thus, during early afternoon, dry and wet conditions had a different impact on the 2 species. Almost all blue sea kraits were concealed and inactive in the afternoon, but they massively emerged in the open during the rain. Several yellow sea-kraits were already active at the same time during dry periods, and many sheltered individuals became easily visible under wet conditions.

3.5 Influence of sex and age classes

For the next analyses, we did not restrict the analyses to any time slot as we focused on the effect of rain without considering the time patterns; however we excluded hidden snakes to focus on the snakes that emerged during wet conditions. The proportion of females relative to males increased during the wet surveys. We counted respectively 19% of females under dry weather (N=2,899) but this proportion increased to 31% during the rain and drizzle (N=415; χ^2=28.1, df=1, P<0001). Interestingly, such effect was caused by the divergent sex behaviours of one species solely. In the blue kraits, we counted 16% (N=1,958) *versus* 32% (N=120) of females under dry or wet conditions respectively (χ^2=21.4, df=1, P<0.001). Such

proportions were not significantly different whatever the weather for the yellow sea-kraits (27%, N=2,011 and 30%, N=260 respectively; χ^2=0.8, df=1, P=0.363).

Rainfalls had a marked effect on immature snakes. During the dry surveys, we observed 423 immature snakes (120 neonates + 303 juveniles: 15% of the total), and 2,475 adults; however, during the rain we observed 123 immature snakes (51 neonates + 72 juveniles: 28%) and 309 adults. The proportion of each age class varied significantly between the two weather conditions (χ^2=64.5, df=1, P<0.01). Further analyses revealed no specific divergence for this effect (all the proportion remained undistinguishable between the yellow and blue sea kraits). Clearly, during the rain, many otherwise small and very secretive snakes became more visible in the open.

3.6 Why do snakes emerge from their shelter during the rain?

The following analyses are limited to the cases where the behaviour (e.g. drinking, exploring the substrate…) was recorded without the disturbance due to capture. Clearly, the snakes emerged massively from their shelter to drink (Figure 3). During the rain, the snakes were not moving to, or from the sea, as usually observed; they were relatively immobile instead. The vast majority of them, 87%, were drinking (143 snakes observed drinking *versus* 21 not). Fifty snakes have also been observed drinking droplets or from puddles during the first 30 minutes after the rain stopped. Obviously, during the dry days, we never observed any snake drinking (N=1,084; χ^2=1,737.0, df=1, P<0.001, Figure 3). The type of precipitation (rain, drizzle) influenced the proportion of drinking snakes. During rainfalls, 97% (N=122) of the snakes were drinking; such percentage dropped to 66% (N=76) following the 30 minutes after the rain stopped, and to 60% during the drizzles (N=42; χ^2=1,074.3, df=13 P<0.001).

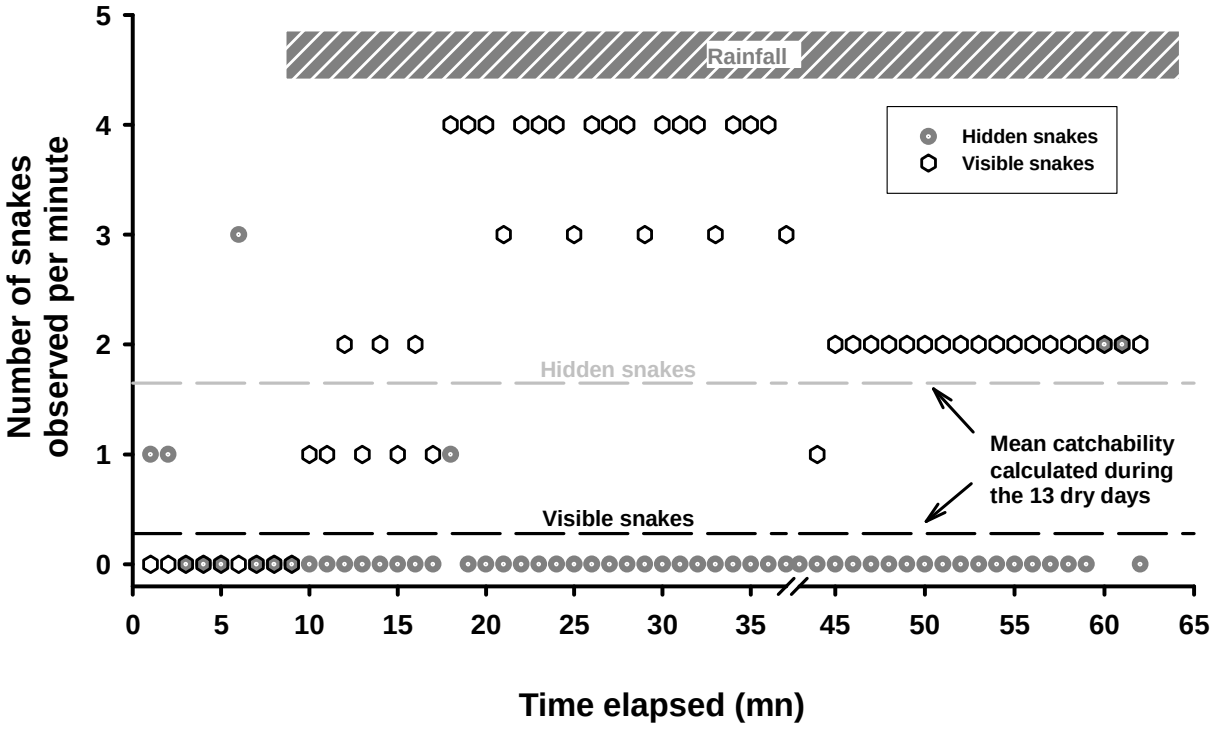

FIG. 3 - *Precise time-pattern of visibility of sea kraits shortly before (10 minutes) and during a strong downpour starting at 17h00 and that finished at 18h00 (rainfalls are indicated by the hatched box). The two species,* L. saintgironsi *and* L. laticaudata*, were pooled together. Each circle provides the number of snakes observed per minute, ranging from zero to four (the maximal value owing to the capacity to observe individuals and to record the data). The open circles refer to the visible snakes (e.g. observed drinking in the open); the grey circles refer to the hidden snakes (e.g. found under flat rocks). The 'X' axis indicates the exact timing during the survey, starting at 17:00 and lasting roughly one hour (the break indicates a short interruption of monitoring). The dashed lines indicate the average catchability of the snakes (# of snakes/min) during the time slot (17:00 – 18:00) under dry conditions over the 13 previous days. The grey line provides the mean value for the snakes found hidden, and the black line provides the mean value for the snakes found visible.*

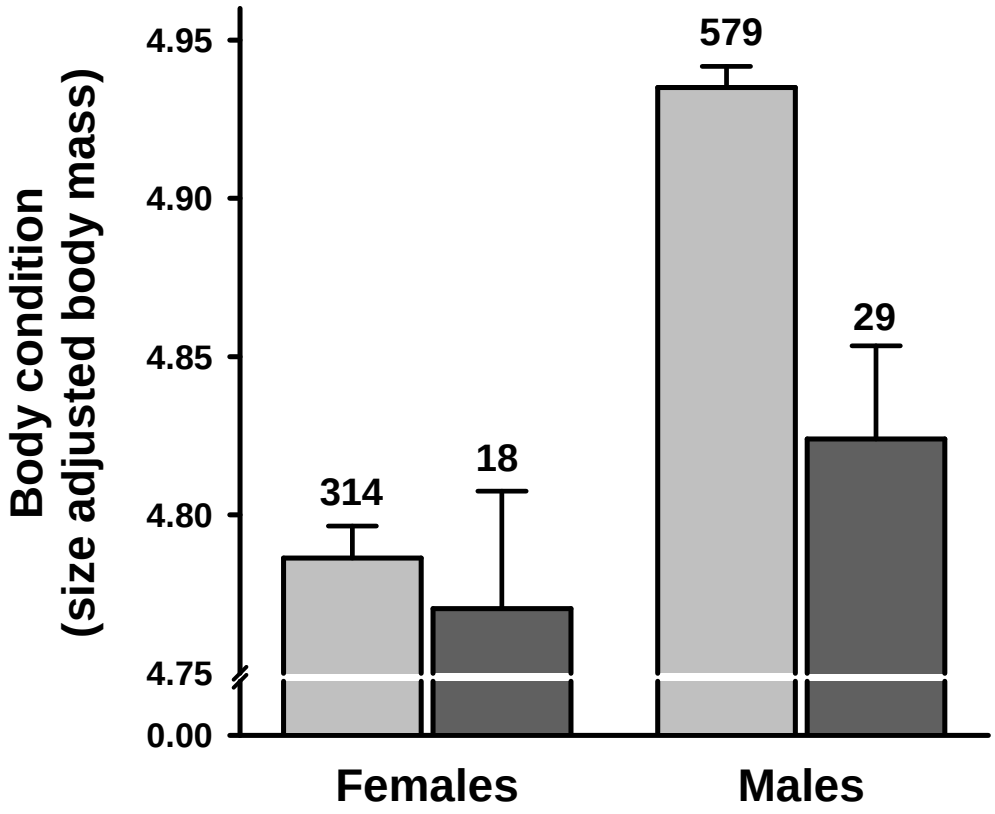

FIG. 4 - *Comparison of the body condition of the snakes (*L. saintgironsi*) captured during dry surveys (light grey bars, the numbers above indicate sample size) and during wet surveys (dark grey bars). Males exhibited higher condition compared to females, and the snakes observed under wet conditions (rainfalls, drizzles…) were in lower condition relative to those captured during dry days (see results).*

3.7 Influence of body condition

Under dry conditions our sample sizes were always large. By contrast, because we favoured behavioural observations over biometric data most of the time during rainfalls, many snakes evaded capture under wet conditions, and therefore we gathered body condition index on a small sub-sample of snakes during wet surveys.

Furthermore, we excluded individuals with a prey in the stomach and gravid females because their size corrected body mass (i.e. body condition index) might only weakly reflects the amount of body reserves (Bonnet et al. 2003). Overall, during the rain we obtained body condition data on 21 *L. laticaudata* (8 females and 13 males) and 47 *L. saintgironsi* (18 females and 29 males). Because both the species and the sex also influence body condition in sea-kraits (Bonnet et al. 2005), the small sample for *L. laticaudata* precluded further analyses (all effect were non-significant, but the power [1-β] of the associated analyses was low). In *L. saintgironsi*, an Ancova was performed with Ln Body mass as the dependent variable, the weather (rain *versus* dry) and the sex as the factors, and Ln SVL as the co-variable: the analysis revealed that the snakes captured during the rain were on average in lower body condition compared to the snakes captured during dry days (effect of the rain: $F_{1, 935}=6.71$, $P=0.01$; effect of the sex: $F_{1, 935}=66.60$, $P<0.001$; interaction: $F_{1, 935}=3.81$, $P=0.05$; Figure 4).

3.8 Do individuals select the best quality water?

To address this question we focused on the surveys during which the exact postures of each snake, and the time at observation were systematically recorded. Under wet conditions the different situations, rainfalls, drizzles and the post-rain humidity of the vegetation triggered peculiar drinking behaviours.

During rainfalls, the first snakes drinking were essentially situated on top of the rocks or logs. For that, they climbed quickly (i.e. as soon as they emerged) onto the nearest relief, positioned their head very close to the top and drunk the water. In comparison to the water running to the base of the rocks, the water collected on the top did not run over the salty substrate (the salt is deposited by the spray, and the tide that covers a large proportion of the shore twice a day). In support of this, after several minutes of strong rain, the snakes went down and almost all individuals were observed drinking from puddles. A logistic regression with the position of the drinking snakes, on the top versus on the ground, as the discrete dependent variable

and the exact time of the observation as the continuous independent variable revealed a significant effect of time (χ^2=19.80, df=1, P<0.0001, Figure 5). At the beginning of the surveys performed under the rain, 64% of the snakes were observed perched on rocks or logs; 30 minutes later this proportion dropped to 24%. Although we had no means to measure the salinity of the water, the strong and continuous rainfall probably washed rapidly the salt from the substrate. The willingness of the snakes to climb rapidly after the beginning of the rain is further illustrated thought an inter-specific comparison. During the strong downpour, within the first 30 minutes of rain, 28 *L. laticaudata* and 30 *L. saintgironsi* managed to reach the top of the rocks to drink. This proportion was very different from that observed during the next half-hour: 38 *L. laticaudata versus* 12 *L. saintgironsi* were drinking form puddles (χ^2=8.7, df=1, P<0.01). The best climbing species (see Bonnet et al. 2005 for a comparison of the climbing abilities) exploited more rapidly the fresh water available on top on the relief whereas the poor climbers relied more heavily on the accumulating water after a delay. Similarly, *L. saintgironsi* represented 96% of all the snakes observed perched on the top of the large boulders in the block field. The only snakes that climb on the trees were all adult *L. saintgironsi.*

During drizzles and after rainfalls, many droplets remained attached to the vegetation. The snakes drunk directly from these droplets, and as a result, many were observed in the thick purslanes that border the shore of our study area (58%, N=126).

Overall, the proportion of snakes perched on the top of the rocks was greater during rainfalls (51%, N=114) compared to drizzles (26%, N=43), and such proportion was even lower after the rain (9%, N 93; χ^2=106.1, df=4, P<0.001). The different percentages of snakes drinking the droplets attached to the purslane leafs mirror this trend: 0% during rainfalls, 35% during drizzles, and 64% after the rain stopped.

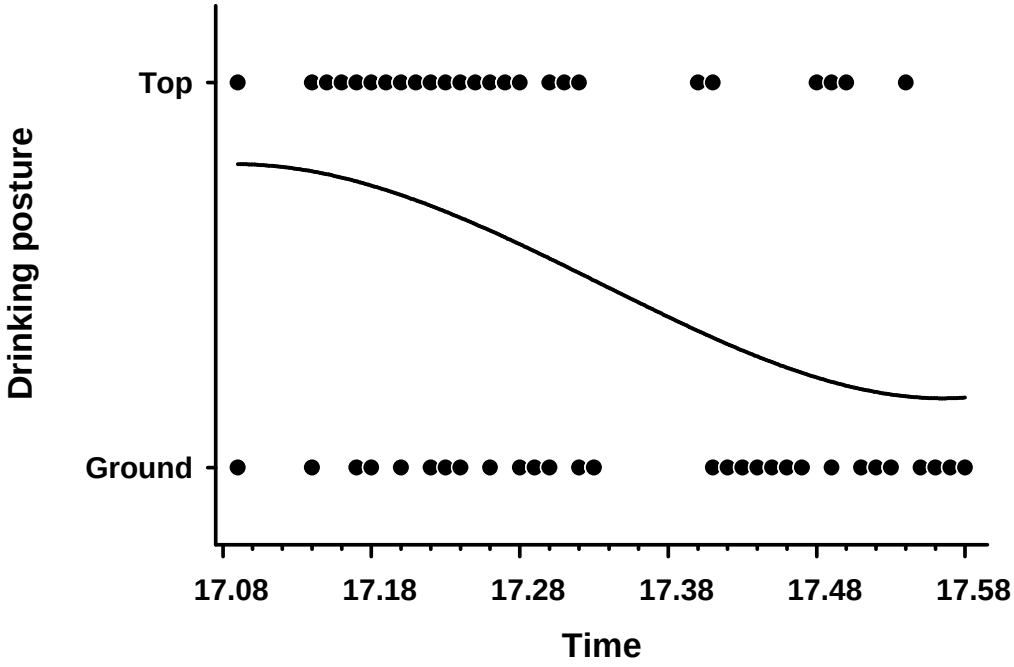

FIG. 5 - *The third of February 2005. During the late afternoon rainfall, many snakes were observed drinking rainwater (N=108, each black circle represents the occurrence of one or more observations). Some of them were perched on the top of the rocks (sometimes logs) to drink the water that had not yet circulated onto the salty substrate (Top on the 'Y' axis, N=58 snakes); other snakes were observed drinking from ephemeral puddles on the flat beach-rocks (Ground on the 'Y' axis, N=50 snakes). The 'X' axis provides the time from the beginning of the rainfall (17:08). The proportion of perched snakes decreased over time, the curve indicating the trend from the logistical regression with the position of the drinking snakes as the dependent variable and the time as the independent variable (see text).*

4 Discussion

To our knowledge, this study provides the first quantitative information on the direct effects of precipitations on drinking behaviours that in turn influence activity patterns of large numbers of individuals monitored in the field. The alternation of droughts and wet conditions had strong impacts on the two species of sea kraits examined, and such effects are likely representative of many animal species that spent most of their time hidden.

Snakes are among the most secretive vertebrates; only strong motivations such as mate searching for example, can force them to abandon their cryptic habits, notably to leave a safe shelter that also provides mild ambient conditions (Bonnet et al. 1999, Shine 2005). Sea kraits exhibited precise timing to undertake displacements between their terrestrial shelter and the sea (Figures1 & 2). The non-random timing of displacements suggests that important benefits are associated with the observed patterns. However, the stochastic availability of fresh-water disrupted the usual pattern of activity. To drink, concealed snakes rapidly left their shelter, remained in the open, and exhibited different types of behaviours, including unusual climbing postures. Such behaviours were systematically and triggered as soon as the water became available (either in the form of running water or droplets) in two snake species. They involved all age/sex classes, and therefore they were likely important. On the other hand, drinking fresh water is not vital to sea snakes as they can expel salt overload through active physiological mechanisms to cope with their marine life and to prolonged droughts when on land. The benefits associated with fresh water intake likely overwhelmed the potential costs associated to forsaking their shelter.

The well-defined general activity patterns of two species of snakes observed over several years, on various sites, and on large samples led to robust patterns. The snakes undertake displacements on land (going to, or coming back from the sea) once a week on average, the typical duration of a foraging trip or of a digestive episode (Shetty & Shine 2002b, Ineich et al., 2007, Brischoux et al. 2007b). In the absence of rain, the majority of the individuals remained concealed. They selected precise time periods, around dusk, to cross the beach. This reinforces the notion that the snakes were very careful with regards to the environmental conditions to move in the open during displacements that lasted only few minutes (sometimes less than a minute, unpublished data) per week. Perhaps that the sea kraits decided to move at dusk and at night, after the sunlight decreased, to limit their visibility with regards to avian predation? Thereby, they may have also avoided the hot summer temperatures of the substrates; we note however that the patterns held true under

dry and cloudy days and that the snakes remained sheltered in the early morning when the substrate was still cool. By contrast, during rainfalls and drizzles the snakes adopted very conspicuous behaviours, remaining motionless and highly visible to drink during prolonged periods.

One of the most surprising behaviour was the eagerness shown by large numbers of individuals to perch on top of rocks and logs as soon as the first drops touched the soil. Sea kraits have the ability to climb steep cliffs; such aptitude is well developed in *L. saintgironsi* but less expressed in *L. laticaudata* (Bonnet et al. 2005). Therefore, it was not surprising to see that many *L. saintgironsi* quickly exploited their climbing talent likely to reach the best quality water. Nonetheless, despite lower abilities, many blue sea kraits managed to perch on the rocks with the head oriented to the top to drink. Such willingness to climb suggests that the snakes somehow estimated that the availability of freshwater was potentially limited in time. After a time delay, the downpours and the strong rainfalls supposedly washed the salt from the surface, and many blue sea kraits came out of their shelter to drink from puddles. By contrast, few yellow sea kraits were observed drinking form puddles, probably because their climbing abilities enabled them to access easily and rapidly freshwater faster as soon as available.

Drinking behaviours during drizzles, or after the rainfalls stopped, brought further evidence that the sea kraits adjust their behaviour with regard to water availability. When the droplets attached to the vegetation was the only accessible form of water, many snakes were observed sucking up patiently one droplet after the next. This was a task time consuming compared to drinking directly from puddle or running water. Because sea kraits can ingest large amounts of water when drinking (unpublished observations), it was not surprising to observe that drinking from droplets was abandoned when puddles and streams were available. Why the sea kraits exhibited both eagerness and complex postures to drink freshwater?

The maintenance of the sea snake hydro-mineral balance is achieved thanks to physiological adaptations (Dunson & Robinson 1976, Heatwole 1999). Sublingual

salt glands expel salt overloads, a process that requires energy expenditure (Potts 1954, Dunson 1968, Dunson & Dunson 1975, Pequeux & Gilles 1978, Shuttleworth & Tompson 1987, Shuttleworth & Hildebrandt 1999, Reina et al. 2002). The high skin surface/body volume ratio of sea snakes entails that significant amounts of Na^+ Cl^- must be permanently expelled, notably during long foraging trips (>10 days, unpublished). If significant amounts of energy can be saved through freshwater drinking, then the individuals in low body condition facing difficulties to maintain their energy budget should also be the most motivated to drink when compared to snakes with large body reserves. The snakes that emerged rapidly from their shelter to drink during rainfalls were in lower body condition compared to the snakes caught under similar conditions but during dry weather. This suggests that the thirstier individuals were also in lower body condition. Although expected, this result is the first (to our knowledge) suggesting a relationship between body reserves and drinking behaviour in natural populations.

Overall, when on land, sea kraits remained concealed under large rocks or within burrows most of the time, probably to avoid overheating, to minimise evaporative water loss, and/or to escape predation. The strong motivation of the snakes to drink intermittent fresh water suggests that they may save sufficient amounts of energy (Nagy & Medica 1986). Such effect combined with irregular precipitations both in their occurrence and form (rainfalls, drizzles) constitute the substrate for natural selection to favour the development of ephemeral, albeit spectacular, drinking behaviours.

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Résumé du Chapitre

Si la vie aquatique des tricots rayés est dédiée à l'acquisition de nourriture, le milieu terrestre est consacré à toutes les autres activités, notamment des activités cruciales telles que la digestion, la mue ou la reproduction.

Tout d'abord, après s'être nourri en mer, les tricots rayés rentrent sur leur îlot. Cette philopatrie avait déjà été soulignée à l'échelle du site (îlot). Dans notre approche, nous avons pu mesurer que les serpents accostent sur une zone très précise de leur îlot. Cette philopatrie à une zone de quelques dizaines de mètres de long, mesurée sur plusieurs années, est remarquable et souligne la sensibilité de ces animaux à de potentiels dérangements et/ou des modifications de cet environnement.

Une fois à terre, les deux espèces de tricots rayés de Nouvelle-Calédonie sélectionnent des habitats bien particuliers. Le tricot rayé bleu reste dans la zone intertidale et sélectionne ses abris (rochers) sur leur taille et sur la hauteur d'eau qui les submergera à marée haute. Ces deux caractéristiques font du tricot rayé bleu un animal inféodé aux îlots qui présentent un type précis de rochers. Le tricot rayé jaune est plus terrestre et moins sélectif. Il rejoint sans difficultés l'intérieur de l'îlot et utilise comme abris indifféremment terriers d'oiseaux marins (puffins du Pacifique, pétrels à ailes noir, pétrels de Tahiti), entrelacs de racines ou amas de roche. Il est cependant très probable que des choix thermiques précis guident cette espèce dans sa sélection de retraites. A l'abri, ces animaux vont digérer, muer, s'accoupler ou pondre…

Le dernier élément examiné sur la vie terrestre des ces animaux concerne une contrainte forte posée par la vie insulaire : les îlots du lagon ne présentent aucun point d'eau douce. Ce manque impose probablement des déviations fortes des paramètres plasmatiques (et notamment la balance hydrominérale) des serpents. Rétablir ces paramètres ou les maintenir dans des gammes compatibles avec la vie impose une dépense d'énergie considérable (élimination du surplus de sel à travers des glandes spécialisées). Les tricots rayés profitent donc d'opportunités rares pour

économiser de l'énergie : les pluies qui leur apportent de l'eau douce. Mais cette manne est imprédictible et impose aux serpents de rompre leur routine (rythme d'activité) pour profiter de cette ressource rare quand elle est disponible.

SYNTHÈSE ET CONCLUSIONS

Tout comme dans le reste du manuscrit, j'ai choisi d'organiser cette dernière partie selon le contraste naturel qui caractérise les tricots rayés : l'utilisation du milieu marin et du milieu terrestre. Globalement, au sein de chacun de ces environnements, il manque des segments qui n'ont pas été examinés au cours de cette thèse. Les informations manquantes seront remplacées par des perspectives de recherche qui permettraient d'éclaircir les éléments absents.

Ecologie marine des tricots rayés

La vie aquatique des tricots rayés est dédiée à l'acquisition de nourriture. Très simplement, les tricots rayés partent en mer, plongent pour chasser des poissons anguilliformes benthiques et rentrent sur leur îlot pour digérer. L'exploration de l'écologie marine des tricots rayés s'est appuyée sur deux outils principaux : d'une part les poissons anguilliformes qui ont servi d'indicateurs, et d'autre part, dans une plus faible mesure, des enregistreurs automatiques de profondeurs (Time-Depth recorders, TDR).

Les données récoltées grâce aux TDR ont permis d'explorer le comportement de plongée des tricots rayés. Les premiers résultats tirés de ces données suggèrent que les deux espèces de tricots rayés auraient des comportements de plongée assez différents. Les tricots rayés jaunes plongeraient plus longtemps et plus profondément que les tricots rayés bleus. Ces résultats préliminaires sont néanmoins assez fragiles (N=1 individu par espèce). L'étude du comportement de plongée nécessitera un investissement massif dans un grand nombre d'enregistreurs miniatures. Les données qui seront récoltées permettront de comparer de manière robuste les deux espèces de tricots rayés de Nouvelle-Calédonie, et au sein de ces espèces, les sexes ou les tailles (âge).

Cependant, les données récoltées grâce à ces appareils nous ont permis d'explorer des aspects plus généraux du comportement de plongée. Les tricots rayés

font preuve d'une endurance extrême : en mer, ils sont capables de passer leur temps à nager et à plonger, nuit et jour, sans aucun repos pendant des durées dépassant dix jours. Les TDR ont détecté des profondeurs de plongée inattendues (plusieurs plongées de plus de 80 mètres, probablement sur le tombant externe du récif-barrière, pour une femelle de *L. saintgironsi*). Les durées d'apnée sont aussi étonnantes pour des animaux qui maintiennent une activité élevée et constante en plongée. La notion classique d'allométrie des capacités de plongée (notamment la durée d'apnée) mise en évidence chez les vertébrés marins endothermes à respiration aérienne (Schreer & Kovacs 1997, Halsey et al. 2006) n'a pas été détectée chez les ectothermes (voir Annexe I). Pourtant, contrairement aux endothermes plongeurs, les ectothermes marins à respiration aérienne ne présentent pas d'adaptations exagérées à la vie marine (voir Annexe I), notamment pour faire face aux pressions hydrostatiques, à la narcose azotée ou l'anaérobie. Comme la taille corporelle influence la plupart des traits d'histoire de vie (Stearns 1992), il est surprenant qu'elle n'agisse pas sur la durée d'apnée chez les ectothermes marins à respiration aérienne. Il est probable qu'un élément clé de leur physiologie nous empêche de détecter l'effet de la taille corporelle sur les capacités d'apnée. Une voie de recherche intéressante pourrait éventuellement s'orienter vers les possibilités de respiration cutanée.

D'autre part, le volet concernant la physiologie de la plongée chez les reptiles marins en général et chez les tricots rayés en particulier est une piste intéressante à explorer. Par exemple, de manière préliminaire, nous avons mesuré chez les tricots rayés un paramètre sanguin (l'hématocrite, pourcentage relatif du volume des érythrocytes par rapport au volume total du sang, Fig 7) qui révèle les capacités à fixer l'oxygène dans le sang. Alors que ce paramètre est très développé chez tous les endothermes marins plongeurs (en comparaison à leurs homologues terrestres, Butler & Jones 1997), les tricots rayés présentent une hématocrite plus faible que les espèces terrestres utilisées dans cette comparaison (Fig 7). De manière intéressante, les tricots rayés jaunes ont une hématocrite plus élevé que les tricots rayés bleus (Fig 7).

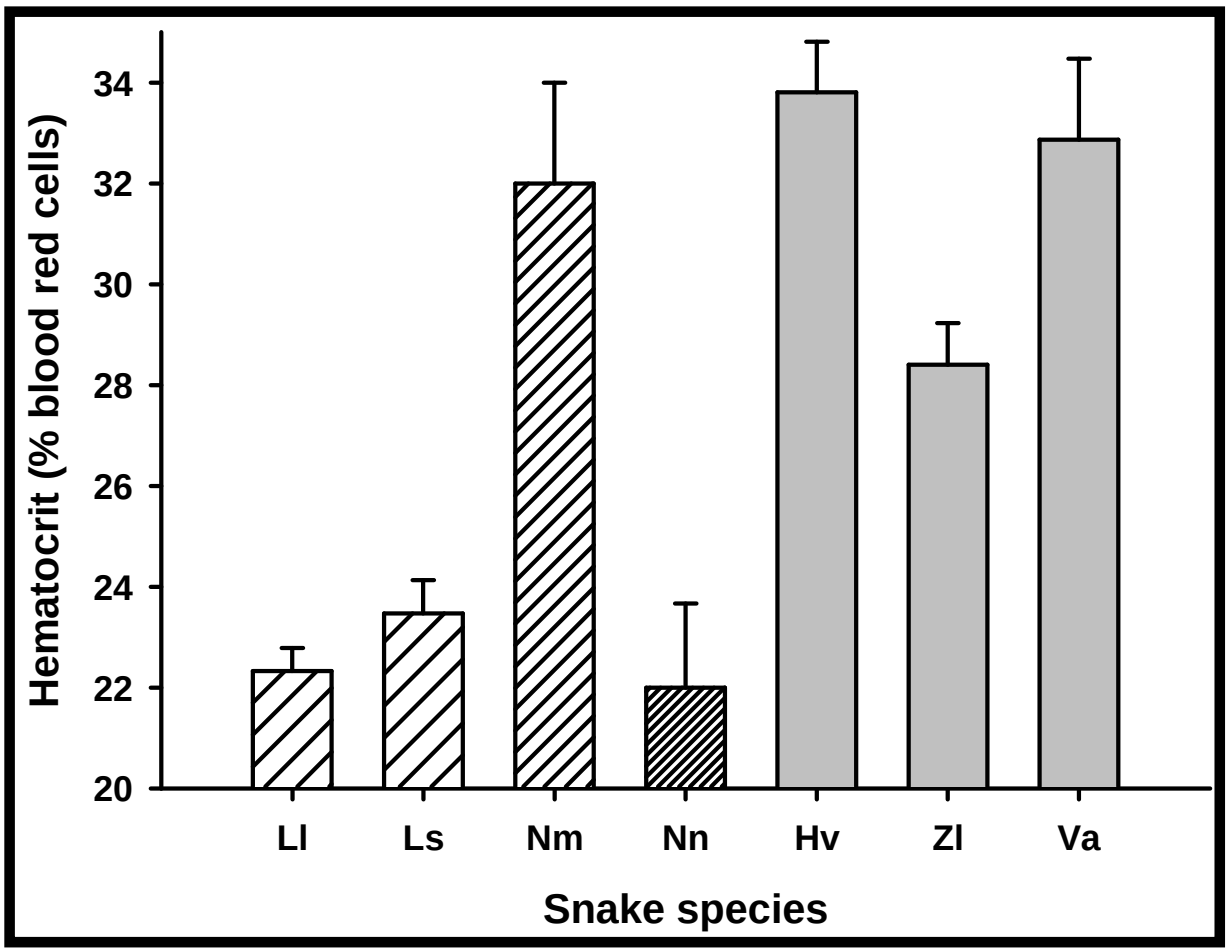

FIG. 7 – Hematocrit level of different snakes species. Species are ranked in relation to their life style (Ll and Ls : *L. laticaudata* and *L. saintgironsi*, marine ; Nm : *Natrix maura*, aquatic ; Nn : *N. natrix*, semi-aquatic ; Hv, Zl and Va : *Hierophis viridiflavus*, *Elaphe [Zamenis] longissima* and *Vipera aspis*, terrestrial).

Si l'utilisation des TDR n'a pas permis d'explorer en détail l'écologie marine des tricots rayés de Nouvelle-Calédonie, leurs proies ont joué un rôle majeur dans la description de leur vie en mer.

La caractérisation du régime alimentaire est une approche classique pour comprendre comment deux espèces coexistent. Très souvent, les ressources trophiques jouent un rôle majeur dans ces situations (Tokeshi 1999). Effectivement, dans notre cas, les deux espèces de tricots rayés de Nouvelle-Calédonie ne consomment pas les mêmes proies (13% de recouvrement entre les régimes alimentaires). Cependant, l'utilisation des proies a été fondamentale pour examiner la plupart des volets de l'écologie marine des tricots rayés. Leur morphologie allongée et donc leur digestion très progressive dans l'estomac des serpents ont été

deux particularités indispensables pour décrire l'écologie alimentaire des tricots rayés.

Ainsi, en combinant vitesse de digestion et état des proies au retour de pêche, nous avons pu mesurer la durée du trajet parcouru entre la zone de pêche et l'îlot d'habitation. En utilisant des vitesses de nage, il a été possible de transformer ces temps en distances : certains tricots rayés effectuent des voyages de plus de 70 km pour trouver une proie (38 km retour – multipliés par deux, en imaginant que le serpent ait été directement en ligne droite vers sa zone de pêche, ce qui est assez peu probable). D'autre part, les proies nous ont permis d'identifier les zones de chasse. Ces habitats sont différents entre les tricots rayés jaunes (matrice corallienne) et les tricots rayés bleus (fonds meubles). La taille et le type d'abris dans lesquels se réfugient les proies (habitat de chasse) orientent les choix alimentaires et les changements ontogéniques du régime alimentaire qui se déclinent de manière contrastée chez les deux espèces de tricots rayés.

Ces résultats étaient tirés en grande partie des rares données disponibles sur les habitats des poissons anguilliformes (base de données FishBase, Froese & Pauly 2006). Récemment, des analyses isotopiques (carbone et azote) du sang des tricots rayés sont venues étayer ces résultats. Cette technique est basée sur les différences de rapports isotopiques en fonction du milieu d'où sont tirées les ressources trophiques mais aussi en fonction du niveau trophique des animaux. Brièvement, le rapport isotopique de l'azote ($^{15}N/^{14}N$, $\delta^{15}N$) augmente progressivement à chaque niveau trophique (de 3 à 5‰ entre producteurs et consommateurs, DeNiro & Epstein 1981, Hobson & Clark 1992, Bearhop et al. 2002). En ce qui concerne le carbone, la source principale de variation du ratio $^{13}C/^{12}C$ ($\delta^{13}C$) existe à petite et large échelle et est une conséquence des taux de production primaire (Rau et al. 1992). Ces signatures permettent donc de discriminer les lieux où les animaux se nourrissent.

Dans notre cas, les deux espèces ne présentent pas de différences de signature au niveau de l'azote (Fig 8), ce qui suggère qu'elles se situent au même niveau trophique. En revanche, les signatures en carbone sont différentes et suggèrent des habitats de chasse différents (Fig 8). Les tricots rayés jaunes ont une signature aux

environs de –12‰ $\delta^{13}C$, ce qui correspond à la signature d'algues poussant sur des fonds durs (turf, Carassou et al. données non publiées). Les tricots rayés bleus chassent à la fois des proies de fonds meubles et des proies généralistes (fonds durs et meubles) et leur signature, aux environs de -15‰ $\delta^{13}C$, se trouve à mi-chemin entre les algues de fonds meubles (*Halimeda* sp., -18‰ $\delta^{13}C$) et de fonds durs (Carassou et al. données non publiées).

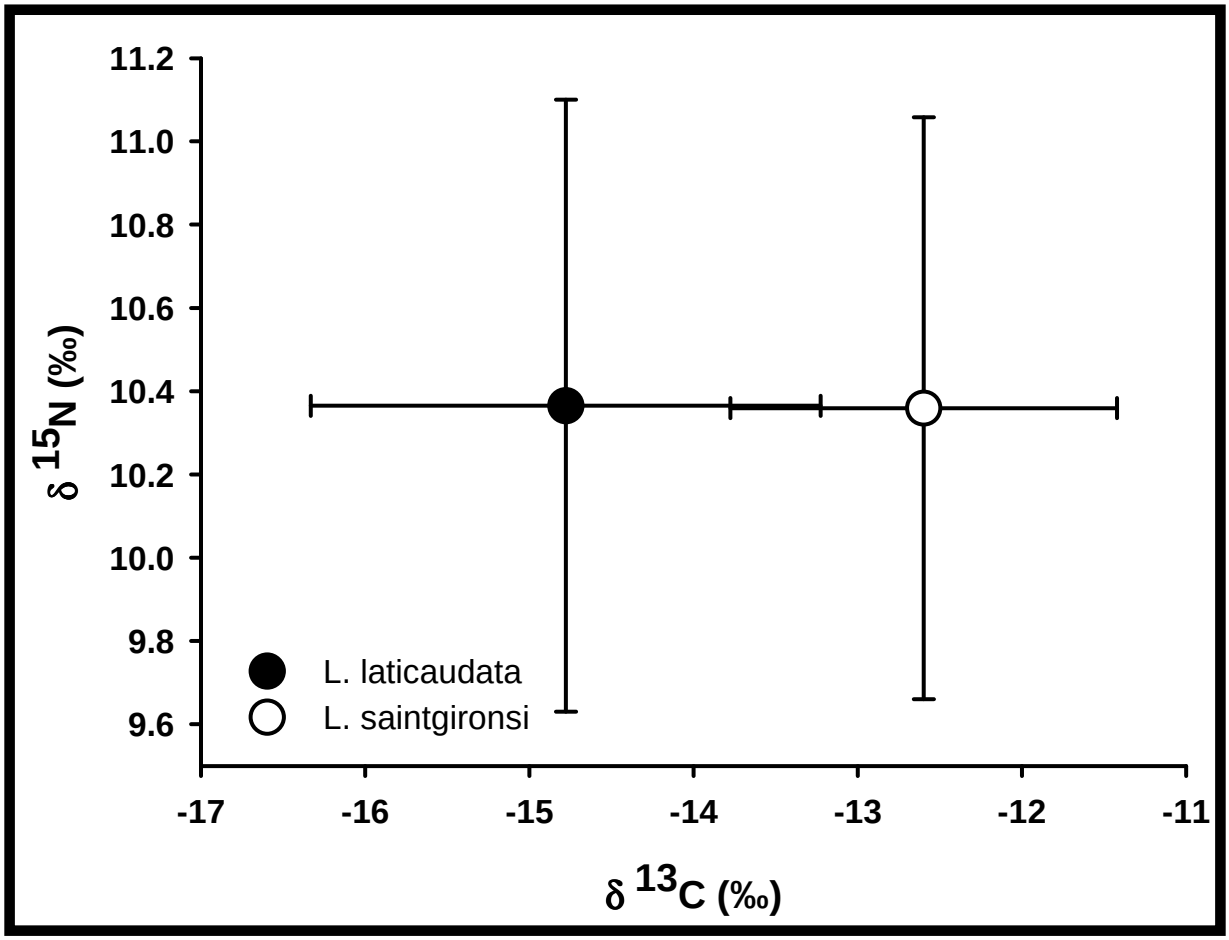

FIG. 8 – Isotopic levels (carbon and nitrogen) of the two sea krait species from New-Caledonia. Each species is represented by 10 adult males and 10 adult females.

Enfin, les proies des tricots rayés ont aussi permis de souligner le potentiel de bio-indication des tricots rayés. Les connaissances sur l'écologie ou la biologie des populations de poissons anguilliformes du lagon de Nouvelle-Calédonie sont peu abondantes (Kulbicki 1997). L'utilisation des tricots rayés de Nouvelle-Calédonie comme échantillonneurs naturels a révélé que la communauté de poissons anguilliformes de Nouvelle-Calédonie présente des abondances plus élevées et une

diversité spécifique plus grande que ce qui avait été estimé jusqu'à présent. Une seule population de tricots rayés consomme entre 900 kilogrammes et 1,5 tonne de ces poissons par an (voir aussi Annexe II). Comme la plupart des îlots de Nouvelle-Calédonie hébergent des tricots rayés, on peut se rendre compte des quantités colossales de poissons anguilliformes consommées par ces prédateurs supérieurs. Quinze espèces, nouvelles pour la zone, ont été identifiées (dont une, *Cirrimaxilla formosa* - 16 individus récoltés, n'était connue que d'un unique spécimen capturé à Taiwan).

L'écologie des poissons anguilliformes est peu connue, mais il sera possible d'utiliser les spécimens récoltés grâce aux tricots rayés pour décrire, du moins en partie, l'écologie des ces poissons (environ 50% des proies collectées ont le corps intact). Il sera probablement possible d'avoir accès à des traits tels que le régime alimentaire ou la maturité sexuelle par exemple.

D'autre part, les tricots rayés pourraient devenir des bio-indicateurs de la richesse spécifique des poissons anguilliformes. L'analyse de leur régime alimentaire pour chaque îlot souligne des différences qui pourraient être liées à des assemblages particuliers de poissons anguilliformes autour de chaque site.

En terme de bio-indication, il est nécessaire de passer à l'étape suivante et d'essayer d'utiliser ces animaux comme indicateurs de l'état de santé du lagon, en dosant des polluants dans les corps gras (faciles à obtenir par biopsie) et en comparant des sites contrastés (près du récif-barrière, au milieu du lagon et près de zones anthropisées – industries et/ou activité minière).

Ecologie terrestre des tricots rayés

L'écologie terrestre des tricots rayés est consacrée à toutes les activités autres que l'acquisition de nourriture, notamment des activités cruciales telles que digestion, mue ou reproduction.

Après la capture d'une proie, les tricots rayés rentrent sur leur îlot. Cette fidélité au site avait été montrée par Shetty & Shine (2002a) aux îles Fidji. Lors de notre examen de l'écologie terrestre des tricots rayés de Nouvelle-Calédonie, nous avons mis en évidence que cette philopatrie ne concerne pas uniquement l'îlot mais est également centrée sur une zone très particulière de la plage. Chaque animal doit probablement connaître parfaitement la topologie/morphologie de la plage et accoste "chez lui". La façon dont ces animaux reconnaissent leur zone reste mystérieuse (ainsi que la manière dont ils se repèrent au milieu des centaines de kilomètres carrés du lagon qu'ils prospectent). Cette philopatrie a bien sûr des conséquences très fortes sur la conservation de ces animaux. D'éventuelles modifications de la plage (dues aux activités touristiques par exemple) auront des répercussions importantes sur les populations de tricots rayés. Deux des îlots prospectés en sont probablement la preuve. Konduyo, qui a été habité pendant plusieurs dizaines d'années, n'abrite aucune population de tricots rayé malgré son apparence accueillante pour ces animaux et la proximité d'îlots peuplés de tricots rayés (à moins de 5 Km, N'Digoro par exemple). En outre, Maître, îlot-réserve sacrifié pour le tourisme, a vu sa population de tricots rayés diminuer très fortement. Mais il manque les données permettant de confirmer cette hypothèse. Par exemple, il est impossible de savoir si Konduyo abritait effectivement une population de tricots rayés avant l'arrivée d'habitants, même si c'est probable. De la même manière, il n'existe pas de données permettant d'étayer l'impression de diminution de la population de tricots rayés de l'îlot Maître…

La fidélité des tricots rayés à une zone particulière de l'îlot est vraisemblablement très avantageuse pour réduire le temps de transit entre la mer et les abris sur l'ilot. Cette réduction du temps de transit permet de réduire l'exposition des serpents à d'éventuels prédateurs, de limiter les pertes hydriques et/ou l'augmentation trop forte de la température corporelle et d'atteindre rapidement un abri qui rassemble des conditions hydriques et thermiques optimales.

La sélection de l'habitat terrestre (abris) est très précise, notamment chez les tricots rayés bleus. Ils restent principalement dans la zone intertidale, cachés sous

des rochers. Ces rochers sont précisément sélectionnés sur leur taille (et donc leur capacité à atténuer des variations de température importantes), mais aussi sur la hauteur d'eau qui les recouvre à marée haute (il faut que les serpents puissent respirer à la surface sans sortir complètement de leurs abris). De manière indirecte, il est probable que les tricots rayés jaunes (rares sous ces rochers) utilisent des habitats terrestres différents (entrelacs de racines, terriers d'oiseaux marins, chaos rocheux) qui sont placés davantage à l'intérieur des îlots.

Enfin, une des contraintes liées à l'habitat terrestre, l'absence d'eau douce, nous a permis d'assister à des comportements très impressionnants lors d'épisodes pluvieux. Les tricots rayés rompent alors complètement leur rythme d'activité classique (tricots rayés bleus nocturnes et tricots rayés jaunes diurnes) et sortent de leurs abris, quelle que soit l'heure. Des quantités impressionnantes de serpents apparaissent soudainement au sol, au sommet de rochers, voire même sur des buissons. La durée de l'épisode pluvieux étant imprédictible et le substrat salé par les embruns, ces animaux commencent par boire l'eau la moins salée en se perchant sur des objets à l'abri des embruns. En fonction de la durée de l'épisode pluvieux, les serpents peuvent éventuellement descendre au sol pour boire l'eau sur un substrat lavé du sel qui le recouvrait. Les tricots rayés jaunes, meilleurs à l'escalade (Bonnet et al. 2005), ont tendance à être plus souvent perchés que les tricots rayés bleus. Ils sont aussi plus rapides et sortent de leurs abris pour boire avant les tricots rayés bleus.

Ce type de comportement suggère que l'acquisition d'eau douce est cruciale pour ces animaux. Ils peuvent survivre à de longues périodes de sécheresse en utilisant leurs glandes à sel, mais probablement au prix d'une dépense d'énergie considérable. Cette dépendance à l'eau douce permet de s'interroger sur les impacts potentiels d'effets climatiques sur les tricots rayés. Par exemple, les épisodes "El Niño" sont caractérisés par une sécheresse intense en Nouvelle-Calédonie. Ces périodes de sécheresses pourraient éventuellement avoir un impact négatif sur les populations de tricots rayés (Fig 9).

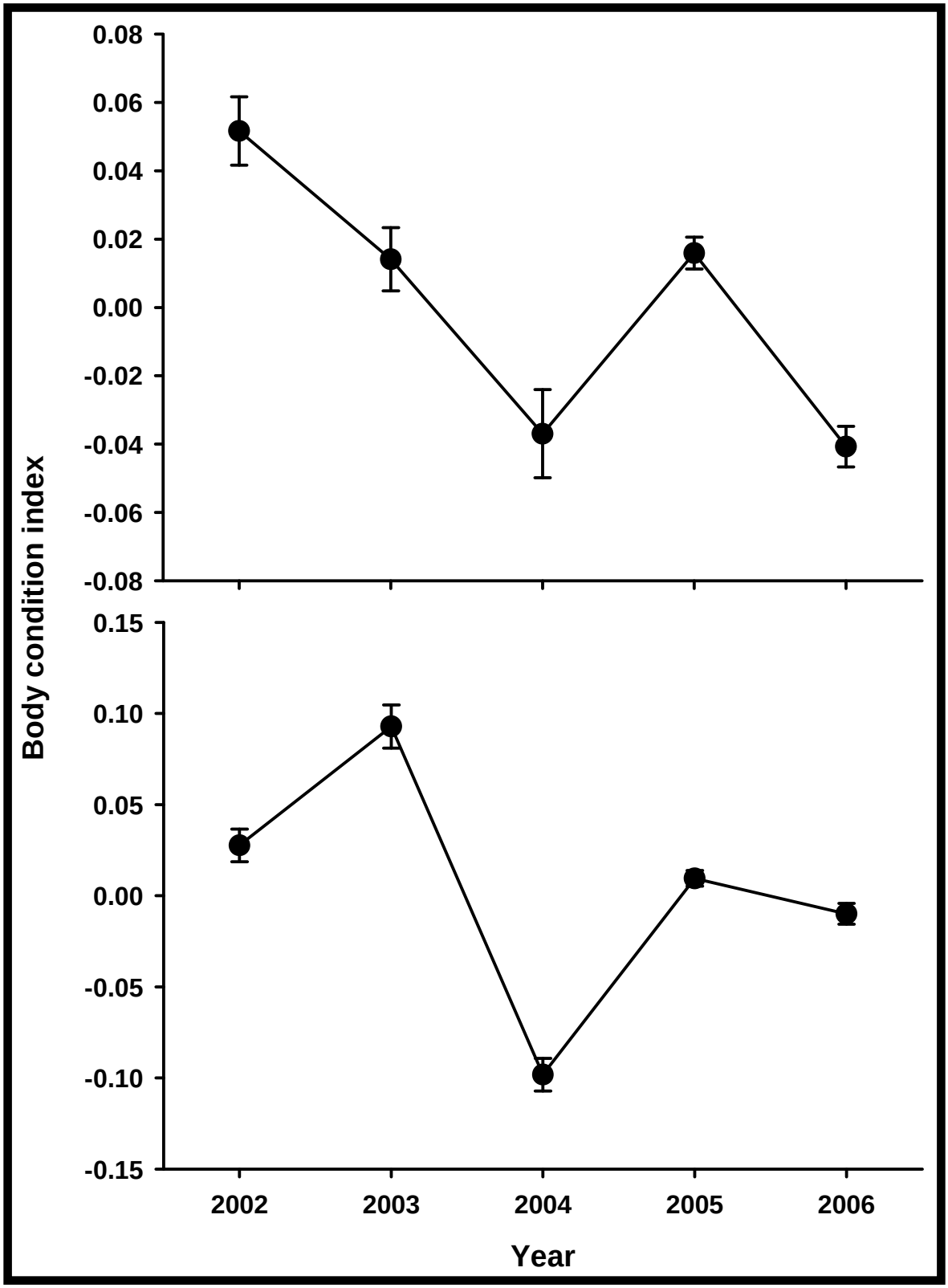

FIG. 9 – Variation of the body condition index of *L. saintgironsi* (upper figure) and *L. laticaudata* between years. Years 2004 and 2006 (low body condition for the two species) correspond to El Niño episods.

Des analyses préliminaires semblent en effet suggérer que les tricots rayés seraient en moins bonne condition corporelle pendant les épisodes "El Niño" (Fig 9). Enfin, il

est évident que la disparition de segments de structures coralliennes (blanchiment) aura un impact considérable sur les poissons anguilliformes et donc sur leurs prédateurs, les tricots rayés.

Conclusions

Le résultat principal de toutes ces explorations est la mise en évidence d'un cortège de différences profondes entre les deux espèces de tricots rayés de Nouvelle-Calédonie. En clair, ces deux espèces n'ont pas du tout la même écologie. Les perspectives qui apparaissent en filigrane derrière ces résultats mettent en jeu une approche complémentaire aux aspects écologiques purs. Les deux espèces de tricots rayés semblent posséder des physiologies et des systèmes énergétiques bien différents. Globalement, il existe une espèce à la fois plus terrestre et plus active en mer : le tricot rayé jaune, et une espèce plus nonchalante dans les deux milieux : le tricot rayé bleu. De telles divergences sont associées à des différences morpho-fonctionnelles et, par exemple, les performances locomotrices des deux espèces coïncident avec leur éco-morphologie (Bonnet et al. 2005). Les réglages physiologiques et métaboliques de ces deux espèces sont probablement bien différents.

Les différences profondes entre ces deux espèces de tricots rayés permettent de comprendre comment ces espèces coexistent. Leurs écologies très différente leur permette d'éviter les effets négatifs des situations de compétition (exclusion compétitive, Grover 1997, Hardin 1960). Il est cependant évident qu'il nous est impossible de statuer sur les relations de causalité : les différences observées entre ces espèces sont elles les causes ou les conséquences de leur coexistence ?

En fait, l'examen d'une seule des situations de coexistence entre membres du groupe des Laticaudidae est probablement insuffisant pour permettre de tirer des

conclusions. Ces situations sont tellement répandues dans la plupart de l'aire de répartition du groupe que seul un examen global permettra d'accumuler certains éléments de réponse.

Diversification des Laticaudidae

Ce qui est frappant au sein de la sous-famille des Laticaudinae, c'est la quantité d'espèces associée à une distribution géographique très étendue (Heatwole 1999). Une autre caractéristique est la diversité des situations de coexistence présentes dans la totalité de l'aire de répartition du groupe. Enfin, ces situations de coexistences multiples mettent en jeu à la fois des espèces appartenant aux mêmes complexes spécifiques mais aussi à des complexes spécifiques différents (voir section Matériels et Méthodes d'Etude).

Ces caractéristiques suggèrent les soubassements évolutifs d'un tel groupe : les processus de radiation adaptative (Schluter 2000). La radiation adaptative est la différenciation, à partir d'un ancêtre commun, d'un nombre d'espèces qui ont colonisé différents environnements. Ce processus inclus l'origine de nouvelles espèces et l'évolution de différences écologiques entre elles. Globalement, la théorie écologique de la radiation évolutive met en jeu des processus de différenciation phénotypique entre les populations, causée directement par des différences dans les environnements colonisés et les ressources consommées (Schluter 2000). Cette théorie et les mécanismes qu'elle suppose pourraient expliquer la diversité des Laticaudinae, la colonisation de nombreux îles et archipels et les situations de coexistence entre membres plus ou moins éloignés du groupe.

La base d'un processus de radiation adaptative est l'apparition d'une innovation-clé et les opportunités écologiques qu'elle offre (Schluter 2000). L'acquisition d'un nouveau trait (innovation-clé) permettrait alors l'occupation de nouvelles niches écologiques, ce qui précipiterait la radiation adaptative. La niche trophique colonisée par les Laticaudinae (spécialisation sur les poissons anguilliformes dans la plupart des cas) et donc la transition partielle vers la vie

marine pourraient vraisemblablement tenir ce rôle d'innovation-clé. A partir d'une telle base, des phénomènes de spéciation allopatrique et/ou sympatrique liés à des épisodes de colonisation/recolonisation permettraient éventuellement d'expliquer la situation actuelle du groupe des Laticaudidae.

Quel que soit le degré de complication ou de sophistication d'un tel scénario, le groupe des Laticaudinae permet de tester ces hypothèses. Cet axe de recherche devrait être constitué de deux volets complémentaires. Une première étape consisterait à clarifier les relations phylogénétiques qui lient les membres du groupe des Laticaudinae. Ces résultats permettraient alors de retracer l'histoire phylogéographique de ce groupe.

Allant de paire avec cet axe "génétique", il sera crucial de décrire l'écologie de toutes les espèces mises en jeu, notamment lorsque les mêmes espèces sont soumises à des environnements différents (environnement physique mais aussi présence d'un ou plusieurs éventuels compétiteurs et différence de degré d'apparentement entre compétiteurs). La confrontation de ces deux approches permettra alors de clarifier les processus qui ont conduit à la diversification du groupe des Laticaudidae.

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Annexes

Allometry of diving capacities: ectothermy versus endothermy

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Abstract. Body mass positively influences diving capacity in air-breathing vertebrates and has been identified as a key determinant for the evolution of diving. Our review on the relationship between body mass and dive duration (a major parameter of dive performance) encompassed for the first time a wide diversity of air-breathing vertebrates. We included a substantial number of non-avian and non-mammalian diving species belonging to phylogenetic lineages that have independently invaded marine habitats (sea-snakes, iguana, turtles, crocodiles). Our analyses suggest that the widely accepted size-dependency of dive duration applies with much less force in ectotherms than in endotherms. Indeed, we failed to detect any effect of body mass on dive duration in ectotherms, possibly because the absence of tight physiological links between body mass and respiratory demands in ectotherms weakens any such correlation. For a more complete understanding of the evolution of diving physiology, future work should encompass both ectothermic and endothermic species

KEY WORDS: diving performance, endothermy, ectothermy, allometry

1 INTRODUCTION

Phylogenetic transitions in habitat use provide exceptionally powerful opportunities to understand the selective pressures operating on morphology, physiology and behaviour. For example, in air-breathing vertebrates, aquatic life exerts major influences on attributes such as the ability to move efficiently through water, to hold the breath in order to remain underwater for long time periods, and to dive to considerable depths (Kooyman, 1989). Some of the most clear-cut examples of adaptation to marine life have been documented in marine endothermic vertebrates: whales, dolphins, seals, penguins, etc. These organisms exhibit major morpho-functional adaptations that considerably increase their diving performance, notably their capacity to remain under water for long periods without breathing, when compared to their terrestrial relatives (Boyd, 1997; Butler & Jones, 1997). However, despite the effectiveness of these adaptations, air-breathing endotherms are highly constrained in dive duration and depth (Butler & Jones, 1997).

Using a large data set, recent reviews (Schreer & Kovacs, 1997; Halsey et al., 2006a, b) have identified a strong and consistent correlation between dive duration and body mass. In endotherms adapted to aquatic life, body size is inversely correlated to relative metabolic rate and positively correlated with relative oxygen stores. Large animals can therefore hold their breath and dive for longer absolute periods than can small species. As expected, they can also reach greater depths and hence can access a wider range of foraging sites. Although highly oriented towards endothermic vertebrates (because these organisms have been intensively studied), a previous review (Schreer & Kovacs, 1997) incorporated some air-breathing diving ectotherms (several sea turtles). The main trend identified in endotherms remained identical: body mass-corrected dive durations of turtles fell within the range of those observed in mammals and birds. Consequently, a strong relationship between body

size and dive duration was proposed as a general rule for air-breathing marine vertebrates (Schreer & Kovacs, 1997; Halsey et al. 2006a, b).

However, we would not expect such a general rule to apply equally in all air-breathing vertebrates. Constraints on dive duration should apply with much less force to ectotherms than to endotherms. Notably, the low metabolic rate of ectotherms, relative to endotherms, reduces their oxygen demands (Pough, 1980). Similarly, the marked flexibility of ectothermic vertebrates for almost all physiological parameters (body temperature, anoxia, acidosis, glycaemia; Belkin, 1963; Shelton & Boutilier, 1982) suggests that the influence of body mass *per se* on dive duration should be relaxed in ectotherms compared to endotherms. Consequently, we expect that an ectothermic air-breathing vertebrate should be able to remain under water without breathing for longer than could a similar-sized endotherm. In the current review, we incorporated a substantial sample of air breathing ectothermic vertebrates, both in terms of body size and taxonomic diversity, in order to examine the relationship between body mass and dive duration. Our analyses show that diving ectothermic vertebrates diverge markedly from the classical trends exhibited by the more intensively studied marine endotherms, and challenge the widely accepted notion that body size is the main predictor for dive duration in air breathing aquatic vertebrates.

2 MATERIAL AND METHODS

2.1 Data collection

Data on body mass and maximum diving duration were collected from the literature. As a basis, we used one of the most complete reviews on diving performances of aquatic air-breathing vertebrates (Schreer & Kovacs, 1997). From this starting point, we added as many additional sources as possible. Due to an accelerating development of bio-logging techniques, the rate of acquisition of novel results has increased rapidly over the last ten years (Ropert-Coudert & Wilson,

2005). We therefore updated previous data sets using recent studies in mammals and birds available in a comprehensive database on air-breathing divers (Ropert-Coudert et al., 2006; online appendix).

The taxonomic diversity of ectothermic vertebrates is poorly reflected by the confusing terminology associated with the words amphibians, reptiles, birds and mammals (see Tree of Life, http://www.tolweb.org). For example, crocodiles are more closely related to birds than to lizards (Hedges & Poling 1999). Nonetheless, the term "reptiles" is still often employed as if it had a phylogenetic validity. Any attempt to explore the morpho-functional implications imposed by marine habitat on air-breathing vertebrate should embrace a wide taxonomic diversity to take into account the phylogeny of vertebrates. Owing to a deficit of data, and to a scientific lack of interest for ectotherms (Bonnet et al., 2002), ours is the first such attempt to review the topic from this perspective. Incorporating new results on ectothermic air–breathing diving vertebrates thus is the most innovative contribution of the present study; we now present data for freshwater turtles, marine iguanas, saltwater crocodiles, freshwater crocodiles and sea snakes (Hobson, 1965; Heatwole, 1975; Grigg et al., 1985; Rubinoff et al., 1986; Van Dam & Diez, 1996; Schreer & Kovacs, 1997; Gordos & Franklin, 2002; Hays et al., 2004; Hochscheid et al., 2005; Seebacher et al., 2005; Sale et al., 2006; McMahon et al., 2007). Finally, we have included our own unpublished data on a species of sea krait (*Laticauda saintgironsi*, FB, XB, TRC, RS, unpublished).

2.2 Selection of the data

The method employed by the researchers to measure diving performance was an important criterion for our selection of data. For both ectotherms and endotherms, we used only studies where animals dived voluntarily. Cases where animals were forced to remain under water (sometimes leading to death) were not retained for our analyses. The rationale for omission of forced submergence studies reflects ethical considerations, as well as the strong biases associated with this technique

(Kooyman, 1985). We also excluded studies on ectotherms monitored while resting or hibernating (e. g. freshwater turtles; Ultsch, 2006) and restricted our analyses to swimming animals because our focus was limited to diving performance.

We selected maximum dive duration as our indicator of diving performance because this parameter directly reflects the upper limits set by diving physiology. Unfortunately, exact maximum dive durations are rarely recorded, and extensive data sets are needed to characterise the actual maximal duration tolerated by animals while diving (e.g. less than 0.01% of all the recorded dives in emperor penguins reached the 22 min maximum dive duration). Because few studies examined diving performance in air-breathing ectotherms, the data available likely underestimate maximum diving performance. As endotherms have been more intensively studied, this sampling bias renders our analyses and main conclusions conservative (see results).

In total, we gathered data on 75 species of mammals, 8 species of turtles, 62 species of birds, 2 species of crocodiles, 1 species of iguana and 11 species of snakes, representing a sum of 25 families belonging to several major phylogenetic lineages that have independently adapted to aquatic habits (online appendix).

2.3 Analyses

Our main aim was to compare the strength of the relationship between body size and dive duration between ectotherms and endotherms. To do so, we analysed the difference in the correlation coefficients for ectotherms *versus* endotherms. In order to quantify the reliability of this comparison, we performed bootstrap analyses (sampling with replacement) to generate a set of 1,000 Spearman correlations (coefficients of correlation are thus given ± S.D.).

We did not frame our analysis in a phylogenetic context for several reasons. Current phylogenies are very incomplete for many non-mammalian and non-avian lineages (see Tree of Life, http://www.tolweb.org). Several major branches are lacking, or the branch lengths are unreliable. The default method of setting the

length of the multitude of branches involved (see www.tolweb.org) to 1 would have introduced substantial (and unquantified) error. More importantly, our results (see below) clearly show a very strong divergence (indeed, with no overlap) between ectotherms *versus* endotherms in dive durations relative to body size. Superimposing those data on various phylogenetic trees would add no real insight to our assessment. For example, crocodiles clearly fall within the ectothermic group in terms of dive duration/body mass relationship, despite their close relatedness to birds.

3 Results

Pooling all the data, we found a significant correlation between body mass and dive duration (Spearman correlation, r_s=0.53, P<0.001), suggesting that body mass influences dive duration capacities in air-breathing vertebrates. However, when the analyses were performed separately in endotherms *versus* ectotherms, the conclusion above was challenged (Figure 1). A graphical inspection of the data revealed a clear-cut divergence between the ectotherms and the endotherms (Figure 1). All the dive durations measured in ectotherms were longer than those recorded in endotherms. Therefore, we further examined the relationship between body mass and dive duration within each metabolic mode separately.

Considering the endotherms solely, the addition of studies (and families) did not modify the pattern revealed by previous reviews: a strong positive correlation between dive duration and body mass (Spearman correlation, r_s=0.88±0.02, P<0.0001; Figure 1). In ectotherms, no such relationship between body mass and maximum dive duration was detected (Spearman correlation, r_s=0.13±0.21, P=0.44±0.30). The distribution of the data did not overlap between endotherms and ectotherms (Figure 1), and their respective range of Spearman rank correlations generated through bootstraps remained clearly different.

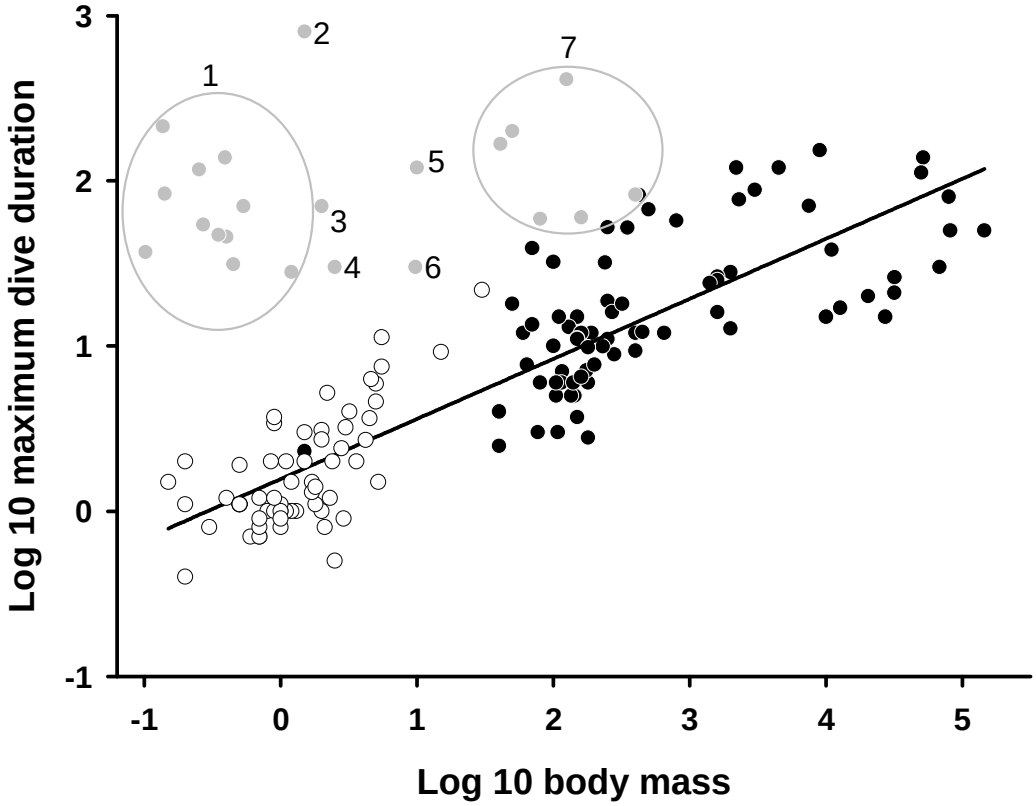

FIG. 1 - *The relationship between maximum dive duration and body mass in air-breathing diving vertebrates from major phylogenetic lineages. White and black circles are for birds and mammals, respectively (regression line for endotherms;* y = 2.91x + 0.2*). Grey circles are for snakes (1), freshwater turtles (2 & 3), marine iguana (4), freshwater crocodile (5), saltwater crocodile (6) and marine turtles (6).*

4 Discussion

Incorporating studies on ectothermic species challenges the generality of the paradigm that diving capacities are constrained by body mass in air-breathing vertebrates (Schreer & Kovacs, 1997; Halsey et al., 2006a, b). The two major recent reviews published respectively in 1997 and 2006a,b provided a baseline to

understand the evolution of this paradigm. The analyses presented by Schreer & Kovacs (1997) provided a general picture where air-breathing diving vertebrates (N>120 species) showed a very convincing overall correlation between body mass and diving performance. However, closer analyses, focused on specific taxonomic groups, sometimes deviated from this general rule; for example, body mass did not appear to be a key determinant of dive duration within otariid seals. This discrepancy between micro-evolutionary and macro-evolutionary processes raises a puzzle: if body mass does not limit diving performance among species within a family, how can this putative influence could apply among families? In a subsequent analysis, Halsey et al. (2006a, b), successfully handled the complexities intrinsic to the analysis of phenotypic data gathered on disparate entities (e.g. small seabirds *versus* giant mammals). Notably, they increased the data set (N=195 species) and framed their analysis within a phylogenetic context. When data on diving performance were controlled for phylogenetic independence, not only were all the above discrepancies resolved, but also most of the mean values for diving variables became statistically indistinguishable between birds and mammals. The authors concluded that body mass was the main determinant of diving performances, and was more important than phylogenetic affinity in this respect (Halsey et al., 2006a, b).

Our analyses with a more diverse data set broadly support many conclusions of the earlier reviews (Schreer & Kovacs, 1997; Halsey et al., 2006a, b). Nevertheless, we emphasize that body size is much less tightly linked to dive duration in ectothermic air breathing vertebrates than in endothermic species. The magnitude of this difference is so striking that it cannot be dismissed as an artifact of the limited number of studies carried out in ectothermic air-breathing diving vertebrates (Figure 1). Hence, the metabolic mode (endothermy or ectothermy) appears to be a major influence on diving performance in air-breathing vertebrates. Hence, future comparisons of various diving traits among species (e.g. respiratory capacities, energy budget…) should incorporate this perspective.

Marine endotherms have been intensively studied, and their remarkable adaptations associated with diving ability have been well documented (see Butler & Jones 1997 for a review). The physiological adaptations of diving endotherms are tightly linked to respiration and metabolism (e.g. increased oxygen stores, reduced global oxygen demands while diving; Boyd, 1997; Butler & Jones, 1997). As a result, the physiological traits involved in respiratory metabolism differ consistently between diving endotherms and their terrestrial relatives.

Although similarly detailed investigations are lacking for air-breathing diving ectotherms, the available information clarifies how ectothermic vertebrates cope with the constraints imposed by diving (Heatwole & Seymour, 1975; Lutz & Bentley, 1985). The most salient element that emerges from the comparison between diving *versus* terrestrial ectothermic vertebrates is an absence of unique, or specific, physiological attributes associated with respiration and metabolism (Heatwole & Seymour, 1975). Major traits linked to lung volume, heart rates, haematological characteristics, or metabolic rates are more influenced by the life style of the species (active *versus* sit-and-wait foragers) rather than by diving (Thompson & Withers, 1997). Most studies have failed to detect any overdevelopment of respiratory capacities in marine reptiles (Heatwole & Seymour, 1975; Lutz & Bentley, 1985; but see Lutcavage et al., 1992 for Leatherback turtles). Apparently, most ectothermic air-breathing vertebrates circumvent the respiratory challenges posed by marine life by exploiting characteristics already well developed in terrestrial species. Notably, ectothermic vertebrates exhibit an extraordinary flexibility with regard to their respiratory physiology: prolonged apnoea, marked bradychardia, or resistance to anoxia (all essential attributes for long dives, Bartholomew & Lasiewski, 1965; Lutcavage et al., 1992; Southwood et al., 1999; Seebacher et al., 2005) are documented in non-diving species also (Belkin, 1963; McDonald, 1974; Heatwole & Seymour, 1975). The conservatism in respiratory capacities in marine ectotherms compared to their terrestrial relatives suggests that the primary adaptations for diving are morphological and behavioural rather than physiological (Heatwole &

Seymour, 1975; Dawson et al., 1977). For example, tolerance to hypoxia is characteristic of most ectotherms regardless of their habitats (Pough, 1980). In combination, these results clarify why ectotherms can consistently outperform endotherms in dive duration (Figure 1).

Nonetheless it would be a mistake to conclude that diving ectothermic vertebrates are not adapted to aquatic life. Body size influences virtually all aspects of the physiology of animals (Peters, 1983; Calder, 1984), in ectotherms as well as endotherms. Clearly, marine ectothermic air-breathing vertebrates exhibit adaptations for aquatic life (e. g. nostril valves, skin permeability, salt glands, paddle shaped limbs or tail). Importantly, the physiology of endotherms isolates them from the environment much more than is the case in ectotherms. For example, the permeable skins of ectotherms, especially in small species (i.e. sea-snakes) allows transcutaneous underwater oxygen absorption and CO_2 elimination (Graham, 1974; Heatwole & Seymour, 1975). This ability clearly can increase dive duration but simultaneously results in less rigid control over hydric and mineral balance; for example, salt penetration through the body wall poses a challenge. Accordingly, all marine ectotherms show specialisations for salt excretion and water conservation (Peaker & Linzell, 1975; Dunson 1978). Interspecific differences in the relationship between body mass/skin surface ratios and diving performance warrant further analysis as potential influences on dive duration, as do factors such as skin thickness, skin permeability and vascularisation, and foraging mode. Variation in such attributes might blur any underlying effect of body mass *per se* on dive duration. If so, the influence of body mass on diving capacities would be more easily revealed through intraspecific studies. As most ectothermic vertebrate species display extensive variation in body size within populations, this hypothesis is readily testable.

Endothermy evolved from ectothermic taxon independently in birds and mammals. The evolution towards endothermy entailed a marked canalisation of many morphological and physiological traits; birds and mammals resemble each

other more in anatomy and physiology than we would expect from their phylogenetic distance (Farmer, 2000). Therefore, the similarity between these two phyla in size-dependency of dive duration is not surprising (Schreer & Kovacs, 1997; Halsey et al., 2006a, b). In strong contrast, ectothermy does not canalise life history traits (Pough, 1980). To more fully understand the evolution of diving physiology, we need to adopt a broad phylogenetic approach that encompasses both ectothermic and endothermic modes.

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Online appendix

List of the families used in this study:

Birds
Anserifromes (Anatidae)
Charadriiformes (Alcidae)
Gaviiformes (Gaviidae)
Pelecaniformes (Sulidae, Phalacrocoracidae)
Podicipediformes (Podicipedidae)
Procellariformes (Pelecanoididae, Procellaridae)
Sphenisciformes (Spheniscidae)

Crocodiles
Crocodylidae

Lizards
Iguanidae

Mammals
Cetaceans (Mysticetes, Odontocetes)
Mustelidae (Lutrinea)
Monotremata (Ornithorhynchidae)
Pinnipeds (Phocidae, Otariidae, Odobenidae)
Sireniens (Dugongidae, Trichechidae)

Snakes
Acrochordidae
Hydrophiidae
Laticaudidae

Turtles
Chelidae
Cheloniidae
Dermochelidae

Annexe I

List of the studies used to gather data on maximum dive duration

Birds:

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Impact of sea kraits on the anguilliform fish community in New Caledonia

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Abstract. The resilience and the functioning of coral reefs depend on the variety and the abundance of predators. It has been recently shown that two communities of predators, the sea kraits and their preys the anguilliform fish, are far more abundant and diverse than previously suspected in many coral reefs of the western Pacific Ocean. Based on the characterisation of the diet, foraging range, feeding rate, and population size of two sea krait species, we estimated the annual offtake of anguilliform fish around Signal Island in New Caledonia. More than 4,000 resident sea snakes take approximately 45,000 fish (>1.5 ton) per year, essentially from 10 supposedly rare fish species. One third is captured on the flat reef, the two other thirds on the soft bottoms within a 17km radius surrounding Signal Island. The multitude of islets of the lagoon that shelter large populations of sea krait, suggests a key role of otherwise neglected predators belonging to two trophic levels: the sea kraits and the anguilliform fish.

KEY WORDS: - Predators, anguilliform fish, *Laticauda*, offtake

1 INTRODUCTION

Predation is recognized as a crucial structuring process in most communities (Carpenter et al. 1985; McCann et al. 1998) including coral reefs (Hixon 1991; Jennings and Polunin 1997). For instance, the number of trophic levels exerts a strong regulatory influence on the whole ecosystem (Finke and Denno 2004). However, given the logistical difficulties to assess simultaneously the complex trophic relationships of various levels, detailed studies on the whole food web interactions are still scarce (Hixon 1991; Caley 1993). In addition, as many predator species are highly cryptic and consequently difficult to sample, their actual impact in the functioning of coral reef ecosystems remains particularly unclear (Kulbicki 1997). Any opportunity to collect substantial amounts information on poorly know, albeit abundant, communities of predators would be useful for a more general understanding of the trophic structures of coral reefs ecosystems.

Such neglected although abundant predator-prey systems have been recently identified in two sites of the western Pacific Ocean: the Republic of Vanuatu and New Caledonia. Diet analysis revealed that the biodiversity and the biomass of at least two trophic levels represented by sea snakes and their preys have been massively underestimated due to the use of inappropriate sampling methods (Reed et al. 2002; Ineich et al. 2007). Four species of sea kraits (Laticaudids sea snakes; *Laticauda colubrina*, *L. frontalis*, *L. saintgironsi*, *L. laticaudata*) occur in very large numbers in many coral reefs and feed on more than 50 species of anguilliform fish that are predators themselves, mostly morays, congers and snake-eels (Reed et al. 2002; Ineich et al. 2007). In New Caledonia, the analysis of the diet of sea kraits revealed 15 new species of anguilliform fish (Ineich et al. 2007; Seret et al. 2007). More generally, large populations of sea kraits are widespread in the Indo-Pacific coral reef areas (Voris 1972; Voris and Voris 1983; Heatwole 1999).

A detailed long-term study suggested that the population of sea kraits from a single islet in New Caledonia might exert an important predation pressure on the surrounding anguilliform fish community (Ineich et al. 2007). The study relied on

various assumptions however. Most notably, the foraging ranges of the sea kraits were unknown and all the estimates were calculated by mixing the two snake species, and by pooling all the different prey species together. Later, further investigations provided information on the specific foraging ecology of the two snake species (Brischoux et al. 2007b). The respective diet, feeding rate and foraging areas exploited by the snakes have been now documented. Simultaneously, mark recapture data collected between 2002 and 2006 on a large number of individuals (>4,000 snakes identified) enables to estimate accurately population sizes. The combination of this information allows estimating more realistically the impact of the sea kraits on their preys. In the current note, a precise evaluation of the impact of sea-kraits on the anguilliform fish community in New Caledonia is proposed with the specific aim to estimate the number and the biomass of more than 40 species of fish eaten by the snakes.

2 MATERIAL AND METHODS

2.1 Sea snakes populations

Two species of sea-kraits co-occur in New Caledonia: one is endemic *L. saintgironsi* (Cogger and Heatwole 2006), the second *L. laticaudata* (Saint Girons 1964; Ineich and Laboute 2002) did not received yet detailed taxonomic attention. Although 10 islets have been sampled, we concentrated most of the research effort on Signal Island (a 6-ha islet situated in the southwest lagoon of New Caledonia; 22°17′45.93 S; 166°17′34.70 E). In this study site, more than 2,600 individuals of these two snake species (*L. saintgironsi*, N=1,246 and *L. laticaudata*, N=1,425) have been individually marked (by scale-clipping) during 6 field trips, from November 2002 to December 2006. The total number of searching days was 177. More than 3,800 recaptures of marked snakes (915 for *L. saintgironsi*, 2,942 for *L. laticaudata*) were obtained. The morphological characteristics of each snake were recorded, notably

snout vent length (SVL), sex, and body mass (further details are provided elsewhere; Brischoux and Bonnet 2007).

Snakes typically exhibit marked time and inter-individual heterogeneities in the probability of capture, accurate population size estimates require to take into account these factors (Bonnet and Naulleau 1996; Bonnet et al. 2002c). During a long field session, 58 consecutive days on Signal Island, the main assumptions to perform population size estimates were met (Otis et al. 1978). On average sea kraits alternate foraging trips at sea with resting periods on land on a two-weeks basis. This means that during short time surveys (i.e. < 1 week), many animals are captured repeatedly because they remain on land whilst roughly half of the snake population evades completely sampling. Therefore, short time sampling sessions tend to miss most of the characteristics of the time-heterogeneity in the probabilities of capture, generating a risk of underestimating the whole population size. The influence of migration and mortality did not complicate the estimates. Indeed, the snake populations were considered as closed because sea kraits tend to be philopatric (Shetty and Shine 2002) and survival is high if calculated during a less than 2 months period (Bonnet et al. 2002c). Population size estimates were performed separately of each species of sea kraits using CAPTURE program software (Otis et al. 1978).

2.2 Quantity and biomass of the prey consumed

The abdomen of each snake was carefully palpated to check for the presence of prey in the stomach. As sea-kraits feed essentially on non-spiny fishes, it was easy to force them to regurgitate (Brischoux and Bonnet 2007). On signal islet, more than 430 prey items were collected, measured and identified (Brischoux et al. 2007a).

Prey size, prey species, and the probability to find a snake with a prey in the stomach, vary with snake body size and snake species in a non-linear way (e.g. certain preys are eaten solely by the adults from one snake species; unpublished data). Therefore it was necessary to run the analysis separately for each snake

species and to take into account the influence of snake body size. For that, the snake's SVL data were divided into classes of 10cm (from 30-40 cm to 110-120 cm in *L. saintgironsi* and to 120-130 cm in *L. laticaudata*). Within each size class, the occurrence and the dimensions of the different preys were calculated. Based on allometric equations, the mean mass of the preys consumed by each size class of snakes was estimated (Brischoux et al. 2007a). The annual consumption of preys was calculated under the notion that on average a snake required 7 days to find, catch a prey and come back on land, plus another week to fully digest it and undertake a new foraging trip (Brischoux et al. 2007b). Therefore, the number (and the biomass) of more than 40 fish species calculated at a given time was multiplied by 26. Overall, such estimates integrated the selection operated by the snakes depending upon their species (dietary specialization), their size (ontogenetic shift), and their respective feeding rate (e.g. small snakes feed more often compared to larger snakes; unpublished data).

3 Results and discussion

The population size estimated on Signal Island was of 4,087 snakes (1,700±96 *L. laticaudata* and 2,387±264 *L. saintgironsi*). A value greater compared to previous estimates (Ineich et al. 2007). The combination of three factors explains such a difference. First, a long time survey enabled to better take into account the marked time heterogeneity of the catchability of the snakes due to their peculiar ecology. Second, the increasing proportion of individually marked snakes over time enabled to process larger number of snakes and to sample the island more systematically and efficiently. Third, the use of a novel technique to catch the snakes based on the lifting of large beach rocks enabled to sample the juvenile snakes more efficiently. Overall, based on five years of surveys, the accuracy of population size estimates was continuously ameliorated and the very high current value of 4,000 snakes for a small island is realistic.

Annexe II

TABLE 1. *List of the prey species of* Laticauda saintgironsi *and* L. laticaudata. *Total number corresponds to the number of prey consumed at any given time (*L. saintgironsi + L. laticaudata*). Total number per year=Total number*26. Biomass was calculated by multiplying total number per year by mean mass of the prey. See text for details on these calculations.*

Prey species	Total number	Total number per year	Biomass (kg)
Anarchias allardicei	11 (4+7)	286	1.3
A. cantonensis	15 (15+0)	405	4.9
A. seychellensis	5 (5+0)	130	0.6
A. sp.	3 (3+0)	78	0.4
Cirrimaxilla formosa	27 (8+19)	702	19.5
Conger sp.	220 (39+181)	5,720	273.3
Echidna sp.	4 (4+0)	104	7.2
E. unicolor	6 (6+0)	156	3.1
Enchelycore pardalis	17 (17+0)	442	3.0
Gymnothorax albimarginatus	171 (0+171)	4,446	325.9
G. chilospilus	499 (463+36)	12,974	260.2
G. cribroris	3 (0+3)	78	5.5
G. eurostus	75 (72+3)	1,950	107.1
G. fimbriatus	75 (75+0)	1,950	81.1
G. formosus	10 (10+0)	260	11.3
G. margaritophorus	72 (72+0)	1,872	84.9
G. moluccensis	61 (3+58)	1,586	62.4
G. nudivomer	7 (0+7)	182	6.0
G. pindae	63 (60+3)	1,638	66.8
G. pseudothyrsoideus	4 (4+0)	104	5.6
G. reevesi	21 (17+4)	546	5.9
G. reticularis	8 (0+8)	208	11.1
G. richardsonii	25 (8+17)	650	13.5
G. sp.1	6 (6+0)	156	2.8
G. sp.2	3 (0+3)	78	3.8

Prey species	Total number	Total number per year	Biomass (kg)
G. undulatus	13 (13+0)	338	7.55
G. zonipectis	8 (8+0)	208	1.6
Muraenichthys sp.	64 (0+64)	1,664	45.6
Myrichtys maculosus	5 (0+5)	130	11.8
Myrophis microchir	68 (0+68)	1,768	53.6
Plotosus lineatus	21 (0+21)	546	3.9
Ptereleotris sp.	18 (0+18)	468	0.6
Scuticaria okinawae	3 (3+0)	78	9.3
S. sp.	3(3+0)	78	2.7
S. tigrina	27 (27+0)	702	65.7
Strophidon sathete	3 (3+0)	78	1.2
Uropterygius alboguttatus	3 (3+0)	78	2.7
U. concolor	24 (18+6)	624	9.4
U. macrocephalus	9 (9+0)	234	3.1
U. sp.	6 (6+0)	156	4.3
U. supraforatus	25 (25+0)	650	21.6
U. xanthopterus	8 (8+0)	208	5.5
Unidentified fish	6 (0+6)	156	4.8
Total	1,725 (1,017+708)	44,865	1,662.2

The precise characterisation of the sea kraits diet (Brischoux et al. 2007b) combined with population size estimates revealed that the sea kraits take a huge quantity of fish per annum, both in terms of number and biomass (Table 1). The impact of the snakes was particularly oriented toward 10 fish species (estimates >1,000 individuals consumed per year), with one species being under strong pressure (*Gymnothorax chilopsilus*; >10,000 fish killed by the snakes from Signal island). Because these fish species are also the main preys consumed by sea kraits from other islets, they must occur in large numbers to sustain the impact of the snakes. However classical sampling methods (under water visual census or

rotenone poisoning; Kulbicki 1997) provided a very different picture. Few anguilliform fish have been identified despite a massive sampling effort: 364 anguilliform fish during >1,350 surveys (Ineich et al. 2007), and less than 150 specimens among the 10 species frequently caught by the snakes (e.g. only 22 *G. chilopsilus*, Kulbicki com. pers.). Several species were found in the stomach of the snake solely (e.g. *Cirrimaxilla Formosa*; Seret et al. 2007).

Each sea krait species selects a particular habitat to forage (hard *versus* soft bottoms) and prospect both on the vicinity and at distance from their home-islet (Brischoux et al. 2007b). One third of the preys are taken on the 130 ha reef flat around Signal islet (Andréfouët pers. com.), representing approximately 15,000 preys (44,865/3) per year. The remaining 30,000 fishes (1 ton) are taken during longer trips within a mean radius of 17km from the islet (Brischoux et al. 2007b). Therefore the impact of the sea kraits is important both in the reef flats and in the soft bottoms of the lagoon.

Although the research effort on the other islets sampled was less intensive, Signal Island might not be exceptional in terms of the number of snakes sheltered. Indeed, in all the islets visited, except one (N=10), large populations were observed and many islets well renowned for their very high snake densities have not been surveyed yet. It is therefore likely that the whole sea krait populations of lagoon of New Caledonia are represented by several tens (hundreds?) of thousands of individuals. Inevitably, the foraging areas of the different populations should greatly overlap; the total impact of sea kraits on anguilliform fish may be very important; suggesting key roles of these two communities of predators in the functioning of the coral reefs in New Caledonia.

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Is melanism adaptive in sea kraits?

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Abstract. Ontogenic melanism (progressive darkening of the skin) has been documented in snakes. Black coloration of the skin often compromises the cryptic effects associated with other patterns (e.g. zigzags) and exposes individuals to predation; however, the mortality risk can be balanced, for example by a thermoregulatory advantage during sun basking. Such adaptive context has been proposed to explain the appearance and the maintenance of melanism within snake populations. Based on a very large captures and re-captures sample (>8,000 observations) gathered on two species of sea-kraits (*Laticauda saintgironsi* and *L. laticaudata* in New Caledonia), we observed that melanism occurred in only one species (*L. laticaudata*), was infrequent and concerned adult snakes solely. None of three adaptive hypotheses respectively linked to thermoregulation, predation, or protection against sun radiations, provided a satisfactory account for the occurrence of melanism in our study populations. Therefore, we suggest that melanism was a fortuitous phenomenon.

KEYWORDS: adaptation, colouration, *Laticauda*, melanism, sea snakes

1 INTRODUCTION

Melanism is one of the most obvious and widespread examples of polymorphism in animal populations (Kettlewell, 1973; Futuyma, 1986). Black individuals are often conspicuous, subject to increased predation; consequently, some benefits somehow counterbalance the deleterious effect of melanism. Notably, the thermoregulatory advantage of a dark colouration during sun basking has been documented in ectothermic species (Andren and Nilson, 1981; Gibson and Falls, 1988; Madsen, 1988; Madsen and Stille, 1988; Luiselli, 1992; Bittner et al., 2002). For instance, In *Vipera berus*, black females reproduce more frequently compared to those exhibiting a zigzag dorsal pattern (Capula and Luiselli 1994). Such advantage likely explains why the frequency of melanism increases with latitude and altitude in many reptiles and amphibians (Monney et al., 1995).

In snakes, melanism is a common, complex and highly variable phenomenon. The expression of melanism varies both in terms of the parts of the body affected (back, head, tail…) and in terms of frequency among populations. Black colourations (e.g. tiger snakes [*Notechis sp*.]; black swamp snake [*Seminatrix pygaea cyclas*]) or black patterns (e.g. grass snakes [*Natrix natrix*]; coral snakes [*Micrurus sp*.]; Timber Rattlesnake [*Crotalus horridus*]) are often partly established at birth and remain permanent throughout lifespan. Rapid changes of colouration (minutes, hours), well documented in many animal species (squids, fish, lizards, owing to the displacements of melanin granules within the melanocytes), may also occur in snakes; however, their moderate intensity cannot be associated to melanism (Bagnara and Hadley, 1973; Hedges et al., 1989). Progressive and marked melanism over time has been observed in different snake species. Therefore, the frequency of black individuals increases within older age classes. In fact, the neonates exhibit cryptic colourations (e.g. complex patterns of spots and zigzags); they tend to become darker over time and apparently acquire their final colour at sexual maturity (Naulleau, 1997). In different species, the occurrence of melanism has been

documented in the adults solely, suggesting that the juveniles retain a cryptic coloration until maturity (e.g. *Vipera berus*, *V. aspis*, *Hierophis viridiflavus*). Such ontogenic changes of colouration are likely adaptive (Booth, 1990) as small snakes are more vulnerable to predation than larger ones, which in turn need to reach high body temperatures during reproduction (e.g. during vitellogenesis; Nagy, 2000; Creer, 2005). In the current manuscript, we report cases of relatively rapid melanism that took place after maturity in already large and sexually mature snakes.

2 MATERIAL AND METHODS

Since 2002, we set up a long-term mark recapture study in 8 islets in the south-west lagoon of New Caledonia: Tenia, Mba, Signal, Larégnère, Porc-Epic, Amédée, Bayonnaise and Brosse (from north to south). We have individually and permanently marked more than 4,700 sea kraits belonging to two species (>2,200 *Laticauda laticaudata* and >2,550 *L. saintgironsi*). Each individual was sexed and measured (snout-vent length SVL±1cm; body mass ±1g).

SVL permitted to assign to each individual an estimated age-class: snakes smaller than 50cm in SVL were classified as neonates; snakes above the minimal size for maturity were classified as adults; snakes in between were classified as juveniles. However, females attained maturity at a larger body size (female and male were considered as adult when exceeding 75.5cm and 63.0cm and 88.5cm and 70.0cm in SVL for *L. saintgironsi* and *L. laticaudata* respectively, unpublished data).

The typical colouration of sea kraits is a banded pattern of regularly spaced black rings on a coloured background. The background is blue for *L. laticaudata* and greyish to bright red for *L. saintgironsi* (Brischoux and Bonnet, 2007). For each individual, we also carefully described the distinctive colour pattern: the colour of the background (e.g. light blue, grey, orange), we counted the number of black rings and noted the abnormalities such as y-shaped rings, and we also recorded the number and the position of the small colour marks such as the small dots or dashes

(either dark or light). The number, size and position of recent injuries were recorded. For simplicity, we categorized the individuals into three colour morphs (Figure 1; Table 1).

(a)

(b)

FIG. 1- *(a) Comparison between the normal banded pattern (top) and a melanic snake (bottom). (b) The melanic adult male (# 463) pictured here exhibited a normal banded pattern 312 days before, without any sign of darkening.*

Snakes with a normal banded pattern (= normal snakes): a well-defined alternation of coloured and black rings;

Individuals with a dark dorsal colouration (= dark snakes), but with the rest of the body presenting a normal pattern (e.g. lateral and ventral parts with a blue or yellow background and black rings);

Melanic individuals (=melanic snakes) where the black rings became almost or fully invisible at least on the dorsal and lateral parts of the body, individuals totally black were included in this category.

We never observed any snake with a black, or nearly black pigmentation, on the lateral parts of the body but with the back still normally banded. Therefore, we assumed that the categories 2 and 3 above were representative of two successive stages for a progressive establishment of melanism, starting from the back and spreading progressively towards the ventral parts of the snake.

3 Results and discussion

TABLE 1- *Occurrence of three main colour patterns in Laticauda laticaudata with respect to sex and age. Banded pattern refers to the normal coloration (blue background and black rings); dark individuals exhibited a dark dorsal coloration but the rest of the body was normally banded; in melanic snakes the blue background colour was replaced by a very dark or black pigmentation (see text for details). The values refer to captures only.*

	Females			**Males**		
	Neonates	Juveniles	Adults	Neonates	Juveniles	Adults
Banded	89	349	261	66	195	1107
Dark	1	10	61	0	0	66
Melanic	0	0	1	0	0	8

The very large sample sizes gathered of both snake species provided a satisfactory level of confidence in our ability to detect black individuals. We never observed dark or melanic individuals in *L. saintgironsi*. By contrast, we recorded a substantial number of dark snakes, and several melanic individuals in *L. laticaudata* (Table 1). The occurrence of melanism was low, only 0.4% of captured snakes were

melanic (8 individuals) and only 1 snake was totally black. The absence of dark, or melanic snakes, in *L. saintgironsi* precluded further analyses in this species.

In *L. laticaudata*, the proportions of different colour morphs varied significantly between the sexes (Table 1; χ^2=21.3, df=2, p<0.001) and between the age classes (Table 1; χ^2=44.2, df=4, p<0.001). None of the immature male (neonates or juveniles) presented a dark or melanic coloration; conversely, several immature females (N=11) had a dark dorsal coloration. In adults, the occurrence of a dark dorsal pattern was greater in females (23%) relative to males (6%). We recorded only one melanic female versus 8 males. However, both proportions were low (0.3% versus 0.6% respectively). Overall, our results were somewhat puzzling. However, under the hypothesis that melanism is a progressive phenomenon; the differences between the sexes became easily explainable. Males reach maturity at a smaller body size, and thus before the females (see above). Consequently, most of the males are represented by adults whilst many females remained juveniles for much prolonged time periods. Such sex difference for maturity generated the sex biased proportions of individuals with an equilibrated sex ratio among neonates, but an overrepresentation of the juvenile females and a very large number of adult males (Table 1).

These interpretations are testable: if we were correct, significant differences of body size should be detected. Notably, darker (presumably older) individuals should be larger than the normally coloured ones because growth requires time. Among adults, the dark individuals (dark or melanic) were larger than those exhibiting a normal banded pattern (in females: ANOVA, $F_{1, 2380}$=14.16, p<0.001, mean SVL: 104.1±0.46 cm and 108.1±0.97 cm for blue banded and dark individuals respectively; in males: ANOVA, $F_{1, 463}$=89.9, p<0.001, mean SVL: 84.6±0.13 cm and 89.3±0.48 cm for blue banded and dark individuals respectively). This supports the notion that the amount of black pigmentation progressively increased over time. Interestingly, the snakes became melanic only after sexual maturity, a pattern not well described in snakes (it is usually assumed that melanism takes place around

maturity, not long after). The data and analyses above provide a picture where melanism is a slow process that requires several years after maturity to be expressed. However, our capture-recaptures led to a different perception. Two individuals shifted from a normal blue and black pattern to a melanic pattern within a year time period: one male captured on Signal islet (99 cm SVL), and another male caught on Amédée islet (92 cm SVL) were recaptured after 312 and 373 days respectively: both became melanic. Their identification was confirmed using the number of black rings (still visible on the ventral part) and the number and disposition of scars. All the dark or melanic snakes recaptured later (N=36; 1-3 years later) kept their colouration, or exhibited a darker pattern over time: melanism was irreversible.

The permanent marking of the snakes required scale clipping (following a code) associated to a superficial burning of the targeted scales. In snakes, this technique usually translates into regenerated scales with a distinguishable and permanent novel colour. Interestingly, the new colours of the marked scales were different between the two snake species. In *L. laticaudata*, the black scales sometimes turned into white, but the blue ones became black. Similarly, the scared injuries led to black marks on the blue background. In *L. saintgironsi*, the black scales remained black, the orange (or grey…) scales re-grew with a dark orange colour (Brischoux and Bonnet, 2007). Such species difference in the modification of the coloration for accidental causes accords well with the fact that melanism was observed only in *L. laticaudata*.

Our data clearly demonstrate that moderate to marked melanism (from dark dorsal coloration to full melanism) occurred in the adults of a least one species of sea-kraits, but not in another one. The two species of sea-kraits share many ecological features: they occur on the same islets, they feed on the same prey types (anguilliform fish; Ineich et al., 2007), and they exhibit relatively similar body sizes (Brischoux and Bonnet, 2007). Although they diverge for many traits (exact diet, activity pattern, morphology, reproductive periods…) we found no satisfactory

explanation for the melanism in *L. laticaudata*. Below we review the main hypotheses favouring melanism in snakes:

Thermoregulation: when the snakes are at sea, their colouration has no influence on their body temperature (Shine et al., 2003). When on land the situation is different. However, *L. laticaudata* remain sheltered under large rocks or under seabird burrows and were never observed exposing their body to the sun. In addition, they are not active during the daylight phase (Brischoux and Bonnet, 2007). On the other hand, L. *saintgironsi* is often observed basking in the sun. The advantage associated with melanism for thermoregulation hypothesis can be confidently rejected.

Anti predation: in many aquatic animals a dark dorsal coloration combined with a light (mirrored) ventral pattern afford an effective crypsis against predators (Johnsen and Sosik, 2003). The low frequency of such a putative camouflage in *L. laticaudata*, along with its total absence in *L. saintgironsi* do not support the notion that melanism is an efficient anti-predator strategy in seakraits. Furthermore, the sea kraits with dark back still exhibited a banded belly and the full melanism produced totally black individuals; two patterns incompatible with a cryptic coloration.

Protection against sun damages: suntan is an adaptive response to the deleterious effects of solar radiations (Herbert and Emery, 1990). However, melanism occurred in the nocturnal species (*L. laticaudata*) and not in the diurnal species that often bask in the sun (*L. saintgironsi*). It is unlikely that the dorso-ventral spreading black pigmentation of the skin, documented in the sea kraits, was a response against the damaging effects of the sun.

None of the above hypotheses provided any support to the melanism displayed by *L. laticaudata*. In the absence of explanation, we suggest that this phenomenon is non-adaptive. Overall, at least part of the colour polymorphism of the sea kraits may be fortuitous and may not require an adaptive context.

Acknowledgements. - We thank François Devinck, Claire Goiran and Dominique Ponton (Aquarium de Nouméa, DRN Province Sud, IRD). We are indebted to Rex Cambag who recovered the bâton de mort. We thank the CNRS and the University François Rabelais for funding. The study was carried out under permit number 6024-179/DRN/ENV and # 6024-3601/DRN/ ENV.

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Laticauda saintgironsi (Sea Krait). Predation.

Margot De Crignis, François Brischoux, Xavier Bonnet, Sophie Lorioux

Centre d'Études Biologiques de Chizé – CNRS, 79360, Villiers en Bois, France

Field observations and laboratory experiments indicate that sea snakes quickly and efficiently kill their prey (fishes) by injecting potent venom (Ineich and Laboute 2002. Sea snakes of New Caledonia. IRD et Muséum national d'Histoire naturelle Editions, Collection Faune et flore tropicales, Paris. 302 pp). Rapid death is probably essential to foraging success in sea snakes. If death were delayed (as is the case in most species of terrestrial venomous snakes) the fish might escape and be difficult to locate in the marine environment. Here, we present the first record of any species of sea snake regurgitating a living prey item (Moray Eel, *Gymnothorax undulatus*).

In the course of conducting mark-recapture studies of large populations of *Laticauda saintgironsi* and *Laticauda laticaudata* on Signal Islet, New Caledonia (22.29 S; 166.29 E) we captured an adult male (695 mm SVL) *L. saintgironsi* on 8 December 2005 at 1740 h. While it was coming back from the sea. Immediately after capture, it regurgitated a Moray Eel. Spontaneous regurgitation is uncommon in sea kraits. We have captured over 3,300 sea kraits with prey items in their stomachs and have observed less than 10 spontaneous regurgitations. Upon regurgitation, the eel dropped into shallow (5 cm) and was not easy to catch. We rapidly placed the eel in a container filled with sea-water (which we replaced every 15 min.). Initially, the eel moved slowly but was still able to swim. Multiple bite-marks visible on the body and the eel's behaviour suggest it had been envenomated. The eel became increasingly lethargic over time. After 78 min. it lay on its back, but righted itself after tactile stimulation with a finger. After 95 min. gill (respiratory) movements became almost undetectable. It died 110 min after the regurgitation, very likely due to the effect of the venom. Overall, the eel survived approximately two hours after being bitten, swallowed, and then regurgitated. The eel was deposited in a collection of sea krait prey (# 630) at the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS UPR 1934). Our observations indicate that while the venom of *L. saintgironsi* certainly causes a paralysis (perhaps transitory or partial) it does not necessarily kill prey instantaneously. Such observations also reveal that sea kraits can forage in the close vicinity of their home islands.

Actions de vulgarisation

Nouvelle-Calédonie

« Les enfants n'ont pas tous les préjugés socioculturels des adultes. Ils adorent venir les caresser et n'ont aucune crainte. C'est la preuve que la peur des serpents n'est pas innée. »

Le tricot rayé se fait des amis au phare Amédée

❑ *Sur l'îlot Amédée, depuis mi-février, certains passagers privilégiés du « Mary D » ont pu découvrir tous les secrets du tricot rayé grâce aux interventions de François Brischoux, un scientifique passionné.*

❑ *Légendes et fausses rumeurs sont balayées et chacun a pu toucher en toute sécurité le serpent le plus célèbre de Nouvelle-Calédonie.*

Texte : Sandrine Morel - Photo : DR

Jeudi dernier, îlot Amédée, 14h30. Il arrive, un grand sac en tissu à la main. À l'intérieur, on devine une certaine agitation et l'enchevêtrement de dizaines de formes irrégulières.

François Brischoux est attendu par une petite quinzaine de touristes calédoniens, métropolitains ou australiens, venus découvrir les charmes du phare Amédée, des fonds sous-marins et de la plage de sable blanc qui l'entoure. Ils savent qu'à présent, entre deux animations organisées par le Mary D, ils vont découvrir l'autre attraction qui fait la réputation de l'île : le tricot rayé.

La plupart le connaissent déjà. De vue. Mais les sont légion. François est là pour remettre les choses au point.

Sur la plage, la rencontre est détendue et les touristes très curieux. Pour se faire comprendre de tous, François Brischoux donne ses explications en français et en anglais.

Les tricots rayés bleus vivent la nuit

Une brève présentation, juste de quoi rappeler le sujet de sa thèse - l'écologie des tricots rayés -, et son travail - l'étude des espèces de chaque îlot, le marquage des individus et la prise de mesures -, et le jeune homme entre dans le vif du sujet. Il plonge sa main dans le sac et en ressort, les uns après les autres, la trentaine de serpents contenus dans ce qui se révèle être une taie d'oreiller. Il en a choisi de toutes sortes.

Le tricot rayé orange et noir est le plus connu et beaucoup s'étonnent de n'avoir jamais vu le bleu. Rien de surprenant. « *Car celui-là vit la nuit* », révèle François Brischoux en portant le magnifique serpent devant les yeux ronds des touristes. D'une main, il soutient le cou et la tête du serpent, et la queue de l'autre. « *Attention, il ne faut pas faire comme moi* », rappelle le chercheur en expliquant que manipuler un serpent n'est pas à la portée de tous. Il s'agit de ne pas blesser l'animal, très fragile, ni de risquer une morsure qui même extrêmement rare, serait dangereuse.

Sans crainte, les enfants caressent le serpent

La foule découvre petit à petit d'autres individus. Les bébés suscitent l'émerveillement de la foule : « *J'essaie toujours de montrer des petits, les gens adorent ça.* » Puis c'est le tour des parents. Il détend leur corps pour en montrer la taille. « *Le plus grand que nous avons mesuré faisait 1,40 m.* » Viennent ensuite les détails techniques. « *Pour différencier un mâle et une femelle, il faut regarder la forme de la queue : celle du mâle est plus longue et plus large.* » Rapidement, les touristes prennent la parole pour demander des explications.

Plutôt qu'un long exposé sur le serpent le plus célèbre de Nouvelle-Calédonie, le scientifique cherche à satisfaire la curiosité du public. « *Il y a un manque en ce qui concerne les ouvrages de vulgarisation sur le tricot rayé. Ça m'intéresse de montrer mon travail aux gens et je le fais aussi pour remercier le Mary D, qui facilite mes travaux sur l'îlot* », explique François Brischoux.

Attentifs et émerveillés, les enfants écoutent les secrets du tricot. Sans crainte, ils s'approchent de François. Ils n'ont qu'une envie : toucher le serpent. Pour finalement se rendre compte qu'il n'est ni visqueux ni gluant, ni rugueux ni froid. Mais plutôt « *agréable au toucher* ». De quoi rendre justice à l'un des plus beaux serpents du monde.

Légendes urbaines

Serpent fascinant, potentiellement dangereux mais doux comme un agneau, le tricot rayé fait l'objet d'un nombre incalculable de fausses rumeurs. Certaines sont surprenantes, d'autres absurdes. Toutes témoignent de la passion qui entoure cet emblème du territoire. Réponses aux questions les plus fréquentes.

● Son venin est-il dix fois plus puissant que celui d'un cobra ?
C'est impossible de mesurer la puissance d'un venin lorsqu'il n'est pas destiné aux mêmes proies. Le cobra chasse des mammifères tandis que le tricot rayé s'attaque aux poissons. On ne peut pas les comparer. Mais c'est vrai que la morsure du tricot rayé est dangereuse et son venin puissant.

● Sa morsure est-elle mortelle ?
Pas si elle est soignée rapidement. Le venin du tricot rayé bloque le système respiratoire. Généralement les premiers signes sont une lourdeur des paupières et une difficulté à déglutir.
Il faut tout de suite appeler les urgences. Mais le serpent n'est pas agressif et le dernier accident dû à l'acharnement d'une personne sur la bête, remonte à plus de vingt ans.

● Que mange-t-il ?
Le tricot rayé se nourrit de murènes et de congres. Il débusque les petites espèces ou les petits poissons qui se cachent dans les coraux. D'ailleurs, grâce à lui, on a réussi à trouver onze nouvelles espèces de murènes jusqu'alors inconnues en Nouvelle-Calédonie. Jusqu'à présent, le plus gros poisson que l'étude actuelle ait découvert était un congre de 500 grammes, plus lourd que le serpent lui-même.

● Sa bouche est-elle vraiment si petite qu'il ne peut mordre qu'entre les doigts ?
Bien sûr que non. Comme tous les serpents, le tricot rayé peut ouvrir la gueule à presque 180°. C'est comme ça qu'il peut avaler les poissons qu'il chasse.

● Quand on les tient par la queue, ils ne peuvent pas remonter ?
C'est évidemment faux.

Repères

Rendez-vous cet été

François Brischoux a effectué plusieurs séjours d'une semaine sur l'îlot Amédée depuis la mi-février. De quoi amasser des informations qu'il est maintenant en train de compiler. Il ne devrait donc y retourner qu'aux alentours du mois de décembre afin de poursuivre son travail de terrain. Patience donc pour tous ceux qui souhaiteraient profiter de cette animation originale.

Conférence à l'IRD

Le 31 mai, à 18 heures, dans le cadre des mardis de la découverte, François Brischoux donnera une conférence ouverte au public à l'IRD. Le thème sera évidemment les tricots rayés.

Un îlot « motel »

Pourquoi trouve-t-on tant de tricots rayés au phare Amédée ? La réponse est simple : il s'agit d'une sorte d'îlot « motel ». Chaque îlot possède en fait sa propre population de tricots rayés. Ces serpents sont casaniers, et quand ils vont chasser, ils finissent toujours par rentrer chez eux. Mais au phare Amédée, François Brischoux a trouvé des populations qu'il avait marquées aux îlots Signal ou Porc-Epic. Venus chasser sur la barrière, ils profitent de la position stratégique d'Amédée pour se reposer et digérer tranquillement à proximité du lieu de pêche.

L'individu le plus long mesurait 1,40 m. Les femelles sont en général plus grandes que les mâles.

Conférence découverte sur les tricots rayés à l'IRD

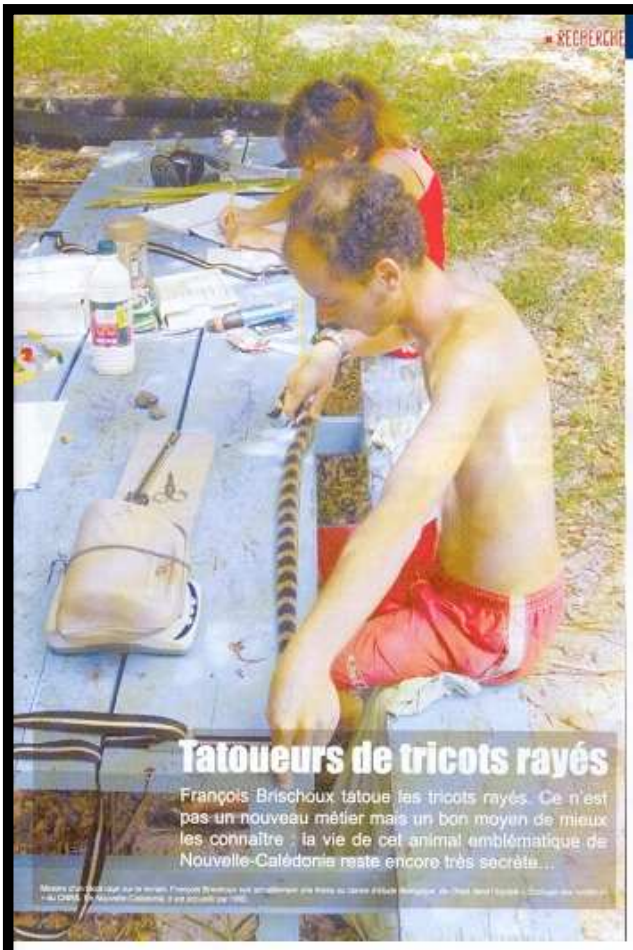
Les serpents marins seront le sujet d'une conférence « Découverte », mardi soir prochain, à 18 heures à l'auditorium de l'Institut pour la recherche et le développement (IRD).

L'intervenant, François Brischoux, doctorant du Centre national de la recherche scientifique (CNRS), en accueil à l'IRD, présentera les résultats de ses travaux sur ces reptiles qui inspirent à la fois fascination et répulsion.

La Nouvelle-Calédonie compte quatorze espèces différentes. La plupart vivent exclusivement en mer, mais deux espèces, communément dénommées tricots rayés, sont amphibies. Peu d'études scientifiques portent sur ces serpents, bien qu'ils soient très abondants et peu farouches. Pourtant, leur mode de vie particulier (terrestre et marin), ainsi que leur abondance, en font des animaux particulièrement intéressants à observer.

De quoi se nourrissent-ils ? Pourquoi vivent-ils à terre et dans l'eau ? Comment reconnaître les différentes espèces ? Quel est leur rôle au sein de l'écosystème lagonaire? Autant de questions qui seront abordées au cours de la conférence.

C'est en suivant les diverses étapes des études de terrain, de la capture à la relâche, que les diverses facettes de l'écologie des tricots rayés seront présentées. Le public aura ainsi l'occasion de voir démystifiés de nombreux aspects de la vie de ces serpents emblématiques de la Nouvelle-Calédonie.



Tatoueurs de tricots rayés

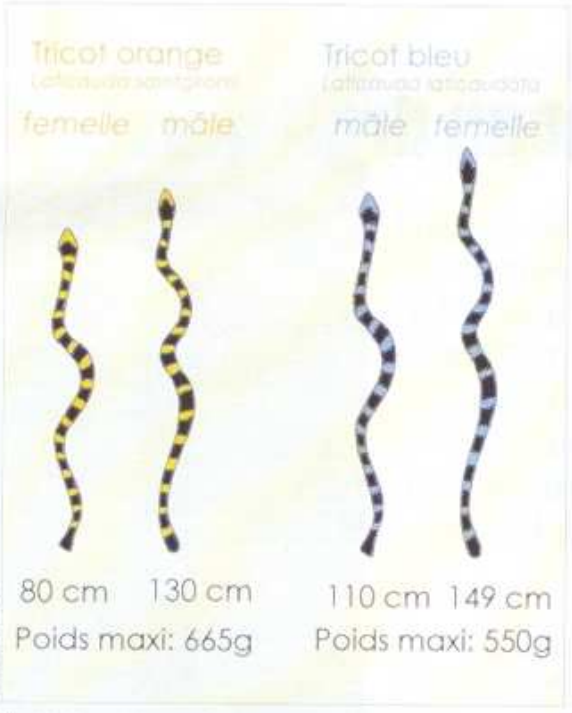
François Brischoux tatoue les tricots rayés. Ce n'est pas un nouveau métier mais un bon moyen de mieux les connaître : la vie de cet animal emblématique de Nouvelle-Calédonie reste encore très secrète...

RECHERCHE

Des proies qui peuvent atteindre 50 à 70% de leur poids

Des régimes différents selon les espèces

Les tricots rayés équipés de sondes



Chez le tricot rayé, deux espèces coexistent, mais elles semblent avoir des habitudes de vie différentes et ne pas se faire concurrence. L'étude menée actuellement par des chercheurs devrait permettre de le confirmer.

le tricot rayé bleu et noir Laticauda laticaudata

pages 30•31

ENVIRONNEMENT

Serpent de mer

Ils fascinent ou ils terrorisent, les serpents font pourtant partie de notre vie. En Nouvelle-Calédonie, les serpents marins sont les plus répandus. On en compte une quinzaine d'espèces réparties sur l'ensemble du territoire. Habitués des îlots et des rives peu fréquentées, le tricot rayé est, à l'instar du cagou, l'un des animaux emblématiques du Caillou.

Le tricot rayé apprécie les îlots pour y nicher, ce qu'il le rend vulnérable à l'activité humaine

A tout seigneur tout honneur, le tricot rayé est incontestablement le plus connu des serpents de Nouvelle-Calédonie, le ou plutôt les tricots rayés puisqu'il en existe deux espèces différentes, le Laticauda colubrina ou tricot rayé commun et le Laticauda laticaudata ou tricot rayé bleu.
Pour le reste, les deux espèces ont un mode de vie assez semblable, ils se nourrissent en mer (notamment de murènes et de congres) mais ils vivent la plupart du temps sur terre pour digérer, muer, se reproduire ou pondre.
Les deux espèces possèdent un venin mortel, y compris pour l'homme, mais les individus ne sont pas agressifs et restent très craintifs.
En revanche, le tricot rayé peut devenir dangereux lorsqu'il se sent dérangé ou menacé, même si les morsures sont extrêmement rares.
Il y a quelques semaines, François Brischoux, doctorant du CNRS, a effectué ses recherches sur les tricots rayés dans le cadre d'une collaboration avec l'IRD. Il est retourné en Métropole poursuivre sa thèse, c'est de là-bas qu'il a répondu à nos questions.

Demain : Combien existe-t-il d'espèces de serpents marins en Nouvelle-Calédonie ?

François Brischoux : 14 espèces dont 2 sont amphibies : les fameux tricots rayés.

Demain : S'agit-il essentiellement de serpents endémiques ?

François Brischoux : Pas forcément, seules 2 ou 3 espèces sont a priori endémiques de la Calédonie (depuis peu de temps le tricot rayé orange). Ces serpents ont habituellement des aires de répartition assez importantes. D'un autre côté, il s'agit probablement du reflet du peu d'études qui ont porté sur ces animaux.

Demain : Le tricot rayé est sans soute le plus connu, quelles sont ses « moeurs » ? Quelle est sa population estimée ? Est-ce une espèce menacée ?

François Brischoux : Les tricots rayés sont effectivement les plus connus en Nouvelle-Calédonie grâce à leurs habitudes amphibies : ils vivent à terre et ne partent en mer que pour se nourrir. Ils sont donc très visibles sur les îlots. Il en existe 2 espèces en Calédonie : le tricot rayé orange, le plus connu et diurne, et le tricot rayé bleu, plus discret car nocturne.
L'impact des activités humaines sur les populations de serpents marins en général et de tricots rayés en particulier (à cause de leur mode de vie amphibie) est certainement très important sur ces animaux : la malveillance, la pollution et surtout la destruction des îlots, comme l'îlot Maître, sont catastrophiques pour ces animaux très sensibles à l'état de santé du lagon. Ils sont d'ailleurs de très bons bio-indicateurs.

Demain : On dit son venin extrêmement dangereux, les archives font-elles état d'accident ? Existe-t-il un sérum ?

François Brischoux : Pour l'instant, à ma connaissance, il n'y a pas eu d'étude sérieuse sur l'impact du venin de tricot rayé sur l'humain (mis à part quelques cas anecdotiques). Ce qui est sûr, c'est que leur venin est très efficace pour maîtriser leurs proies. Le rôle de défense du venin n'est que secondaire, il s'agit avant tout d'une arme redoutable pour chasser sa nourriture.
D'autre part, il existe un sérum, disponible auprès des services d'urgence de Gaston-Bourret par exemple.

Demain : On connaît moins bien les autres espèces, certaines sont-elles 100% marines, l'essentiel de leur cycle biologique se fait-il en mer ?

François Brischoux : Effectivement, elles sont 100% marines et ne viennent jamais à terre. Même la naissance de leurs petits se fait en mer (ce sont des espèces vivipares au contraire des tricots qui sont ovipares).

Demain : Quelles sont leurs habitudes alimentaires ?

François Brischoux : En général, des petits poissons de fond (gobies, blennies,...). Les tricots rayés, quant à eux, sont spécialisés sur les poissons allongés (murènes, congres, poissons serpents). Une espèce du lagon, le serpent à tête de tortue, ne consomme que des oeufs de poissons. ■

***Pour en savoir plus :** « Les serpents marins de Nouvelle-Calédonie » Le livre d'Ivan Ineich et Pierre Laboute (disponible à l'IRD) est une mine d'informations.*

C'est en mer que le tricot rayé trouve l'essentiel de sa subsistance

Les deux tricots rayés de l'îlot Amédée

Tricot rayé jaune

lèvres claires

surtout le jour

plus terrestre

Tricot rayé bleu

lèvres sombres

surtout la nuit

Les tricots rayés ne sont pas farouches et peuvent être observés de très près.

Cependant, il ne faut pas les manipuler car leur morsure peut être dangereuse.

Des serpents amphibies

Les tricots rayés vont en mer pour se nourrir

un tricot et sa proie

muer…

accouplement

en chasse

Ils chassent des murènes et des congres et rentrent a terre pour digérer…

en mue

ou se reproduire.

étude sur l'écologie des tricots rayés est menée par le CNRS en partenariat avec The University of Exeter IRD avec l'aide indispensable de

Annexe V

Liste des Publications

Liste des publications sur la thématique de la thèse

Brischoux F, Bonnet X. 2007. Life history of sea kraits in New Caledonia. Mémoires du Museum National d'Histoire Naturelle, in press.

Brischoux F, Bonnet X, De Crignis M. 2007. A Method to reconstruct anguilliform fishes from partially digested items. Marine Biology, 151:1893-1897.

Brischoux F, Bonnet X, Shine R. 2007. Foraging ecology of sea kraits (*Laticauda* spp.) in the Neo-Caledonian lagoon. Marine Ecology Progress Series, 350:145-151.

Brischoux F, Bonnet X, Cook TR, Shine R. 2007. Allometry of diving capacities: ectothermy versus endothermy. Journal of Evolutionary Biology, 21:324-329.

Brischoux F, Bonnet X, Cook TR, Shine R. 2007. Snakes at sea: diving performances of free-ranging sea kraits. Proceedings of the 11th Annual Meeting on Health, Science & Technology, University François Rabelais, Tours.

De Crignis M, **Brischoux F**, Bonnet X, Lorioux S. 2007. *Laticauda saintgironsi* (sea krait). Predation. Herpetological Review, in press.

Ineich I, Bonnet X, **Brischoux F**, Kulbicki M, Séret B, Shine R. 2007. Anguilliform fishes and sea kraits: neglected predators in coral-reef ecosystems. Marine Biology, 151:793-802.

Lorioux S, Bonnet X, **Brischoux F**, De Crignis M. 2007. Is melanism adaptive in sea kraits? Amphibia-Reptilia, in press.

Seret B, **Brischoux F**, Bonnet X, Shine R. 2007. First record of *Cirrimaxilla formosa* (Teleostei: Muraenidae) from New Caledonia, found in sea snake stomach contents. Cybium, in press.

Autres publications

Ford N B, **Brischoux F**, Lancaster D. 2004. Reproduction in the western cottonmouth, *Agkistrodon piscivorus leucostoma*, in a floodplain forest. The Southwestern Naturalist, 49(4):465–471.

Lourdais O, **Brischoux F**, DeNardo D, Shine R. 2004. Protein catabolism in pregnant snakes (*Epicrates maurus*, Boidae) compromises musculature and performance after reproduction. Journal of Comparative Physiology B, 174:383-391.

Lourdais O, **Brischoux F**, Barantin L. 2005. how to assess musculature and performance in a constricting snake? A case study in the rainbow boa (*Epicrates maurus*). Journal of Zoology, 265:43–51.

Lourdais O, **Brischoux F**, Shine R, Bonnet X. 2005. Adaptive maternal cannibalism in snakes. Biological Journal of The Linnean Society, 84:767-774.

Ineich I, Bonnet X, Shine R, Shine T, **Brischoux F**, LeBreton M, Chirio L. 2006. What, if anything, is a "typical viper"? Biological attributes of basal viperid snakes (genus *Causus*, Wagler 1830). Biological Journal of The Linnean Society, 89:575-588.

Lourdais O, Shine R, Bonnet X, **Brischoux F**. 2006. Sex differences in body composition, performances and behaviour in the colombian rainbow boa (*Epicrates cenchria maurus*, Boidae). Journal of Zoology, 269:175–182.

Travaux actuellement soumis

Bonnet X, **Brischoux F**. Thirsty sea snakes forsake their shelter during rainfall. Submitted to Austral Ecology.

Brischoux F, Bonnet X, Shine R. Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. Submitted to Marine Ecology Progress Series.

Brischoux F, Bonnet X. Impact of sea kraits on the anguilliform fish community in New-Caledonia. Submitted to Population Ecology.